Online optimisation of information transmission in stochastic spiking neural systems

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Abstract

An Information Theoretic approach is used for studying the effect of noise on various spiking neural systems. Detailed statistical analyses of neural behaviour under the influence of stochasticity are carried out and their results related to other work and also biological neural networks. The neurocomputational capabilities of the neural systems under study are put on an absolute scale. This approach was also used in order to develop an optimisation framework.

A proof-of-concept algorithm is designed, based on information theory and the coding fraction, which optimises noise through maximising information throughput. The algorithm is applied with success to a single neuron and then generalised to an entire neural population with various structural characteristics (feedforward, lateral, recurrent connections).

It is shown that there are certain positive and persistent phenomena due to noise in spiking neural networks and that these phenomena can be observed even under simplified conditions and therefore exploited. The transition is made from detailed and computationally expensive tools to efficient approximations. These phenomena are shown to be persistent and exploitable under a variety of circumstances.

The results of this work provide evidence that noise can be optimised online in both single neurons and neural populations of varying structures.

Declaration of originality

I hereby declare that the research recorded in this thesis and the thesis itself was composed and originated entirely by myself in the School of Engineering at The University of Edinburgh.

Alexandros Kourkoulas Chondrorizos

Acknowledgements

I dedicate this work to V. who crossed a whole continent to be with me.

I would like to thank Alan F. Murray for being the best supervisor I have ever had and could possibly hope for and also for restoring my faith in academics.

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Acronyms and abbreviations

IF	Integrate and Fire
SR	Stochastic Resonance
IT	Information Theory
MI	Mutual Information
HH	Hodgkin and Huxley
WK	Wiener-Kolmogorov

Chapter 1
Introduction

Neural networks are powerful computational systems. Their impressive computational capabilities are achieved by combining large numbers of small yet complex computational units called neurons. The distinguishing characteristic of neurons, as computational units, is that they communicate with each other incredibly quickly. This interplay between vast numbers of units communicating rapidly creates a fertile substrate for powerful computation. Ever since the basic working principles of neurons and their populations were understood and the very first computers were developed, understanding and replicating the way neural systems work has been a focus of research. Knowledge of the biophysics of neurons and their networks is beyond extensive and extremely accurate models can be now built. However, there is no single universal neuron model, as there is no single universal neuron. Just as there are neurons with different properties performing different tasks, there is a variety of neural models. These models define a range of detail and efficiency. At one end, there are models which are as biologically accurate as possible in an attempt to encapsulate all of the neural properties that give rise to the complex behaviour of neurons and their ensembles. At the other, there are simplistic neural models which capture the bare essentials with the purpose of building large populations of these models in an attempt to look at the bigger picture. There are numerous models at different points on this spectrum and researchers tend to pick the one that fits the scope of their research best.

If biological plausibility is within the scope of one's research then it logically follows that one should pick a neuron model, and more generally a framework, which embodies principles and notions found in real, biological neural systems.

One of these notions is noise or stochasticity. Neural activity is unreliable. Mistakes are a very common occurrence in the nervous system and there are a variety of phenomena and processes that, intuitively, should work in a detrimental way for its computational processes. However, reality contradicts intuition in this case. Noise has changed notionally for neural systems over the years. It used to be considered a deleterious force, whereas now it is considered to have many positive effects. Slowly, it is changing again. Now it seems possible that noise may

well be a necessary aspect of neural processing. This seems a logical conclusion since neural systems have evolved in extremely noisy environments.

This concept immediately raises some questions. The most important is, how can it be shown whether this is true or not? In other words, what is an appropriate framework for studying the effect of noise on neural systems? Any candidate for this task has to comprise of a set of tools that have been applied to other computational systems. This gauges the notional equivalence of the neural system's computational aspects with those of other computational systems and places them on an absolute scale. This set of tools should also be one that has been applied to other neural systems in the past with known and predictable results.

1.1 Aim

In this body of work, Information Theory, a framework widely used in signal processing and analysis, and its conceptual extensions, are used in order to try and elucidate the effects of noise on spiking neurons and their populations. Also, an analysis of some aspects of this framework as an optimisation tool is carried out. In other words, the aim of this work is to find out if there are any positive effects of noise on spiking neural networks and to see if these phenomena could be harnessed in order to design more powerful computational systems and potentially draw any conclusions about the effect of noise on biological neural networks.

The most important goal of this work is to show that from the variety of tools available for the study of spiking neural networks the most appropriate must be chosen according to the scope of the research at hand. Analytical methods may provide clearer insight as to what is actually happening inside neurons and networks and with a much greater degree of accuracy, but they require large amounts of data. If, on the other hand, the goal is an accurate enough approximation that can be used instantaneously, a different methodology must be chosen. We also aim to show that it is achievable, desirable and biologically plausible that spiking neural networks can possess attributes that allow them to exploit their surrounding stochasticity to improve their information processing capabilities.

The driving hypothesis behind this work is the notion that noise can and does have a constructive effect on certain aspects of a spiking neural population's behaviour. That these effects can be observed and analysed in a variety of systems, that is to say they are generalisable, and that they are exploitable by the neural populations themselves. Also, this work intends to show that

positive stochastic phenomena can be exploited online and in a biologically plausible way.

Previous work has shown that noise has a positive effect on the information transmission of neural systems which is pertinent to this work [10–26]. Establishing that certain stochastic phenomena also occur in complex populations of biologically inspired spiking neurons is an integral part of this work. Some researchers have also attempted to optimise these effects in a variety of ways [8, 11, 17, 18, 27–29]. However, optimisation with respect to noise is elusive. In this work, determining an optimum for noise is not enough. The effect of noise on information transmission is expressed in such a way that optimisation is meaningful and potentially biologically accurate. More importantly, the positive effects of noise must be expressed in such a way that the neural system can take advantage of them immediately and efficiently. In other words, the effects of noise are simplified and made available to the neural system in a biologically plausible way so that online noise optimisation becomes possible.

1.2 Contribution

This work shows that IT is a valuable tool-set if used as the basis for the development of more sophisticated tools. It also shows that online stochastic optimisation is not only feasible but most likely preferable and that this approach is not only more efficient but also, potentially, more biologically plausible. The online optimisation algorithm developed in this work is shown to be generalisable and consequently online noise optimisation is shown to be feasible and effective on both single neurons and neural populations of varying structures. It is also shown that neural system structure and other specific properties determine the effect of noise in such a way that not much is needed in terms of optimisation. This is a rather important notion since it would mean that neural systems have evolved to exploit stochasticity passively, an approach that would be extremely efficient.

1.3 Overview

In Chapter 2 some background is given about spiking neural networks, both biological and artificial. In Chapter 3 noise and its effects on neural systems are reviewed. Chapter 4 deals with Information Theory as a whole and also in how it was applied in the specific case of this work. Chapter 5 analyses the potential of optimising any benefits due to noise, describes an

attempt at designing a simple yet effective online algorithm for this purpose and extends this notion to an entire population of neurons. Chapter 6 discusses the implications of this work and the potential directions it could take.

Chapter 2
Spiking Neural Networks

One of the most important aspects of neurons as computational units is their ability to transmit information rapidly. This information transmission is achieved by the generation of electrical pulses called action potentials, or spikes, which travel along nerve fibres. Information in these signals is represented as patterns and sequences of spikes arranged in space and time in a specific way that encodes characteristics of the variety of signals that the body is exposed to.

2.1 Biological Neurons

2.1.1 Axons and dendrites

Two important parts of the neuron's morphology are the axon and the dendrites. The dendrites usually assume elaborate, branching spatial configurations that allow the neuron to receive input signals from several thousands of other neurons via synaptic connections. The axon carries the output signal of the neuron to other cells. It leaves the cell body of the neuron and can travel large distances through the brain and the body itself [3]. Some typical examples of neurons, their axons and the variety of formations they assume, can be seen in Figure 2.1.

2.1.2 Ion channels

The most obvious characteristic which is integral to the functionality of neurons is ion channels. Ion channels are complex molecules permeating the neuron's cell membrane that control the movement of ions into and out of the cell. The main ions that are involved in this process are sodium (Na^+), potassium (K^+), calcium (Ca^{2+}) and chloride (Cl^-). These channels allow ions to flow across the cell membrane in response to changes in voltage and also a variety of other signals [3].

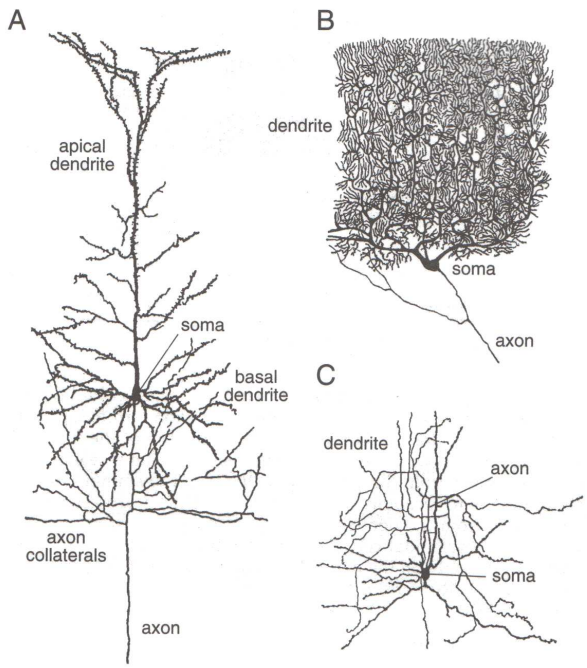

Figure 2.1: *Drawings of three kinds of neurons. A) This is a cortical pyramidal cell. It is one of the primary excitatory cells in the cerebral cortex. Its axons branch locally, forming connections with nearby neurons using axon collaterals. They also project distally, transmitting signals to other parts of the brain and the nervous system. B) A Purkinje cell in the cerebellum. Their axons transmit the output of the cerebellar cortex. C) A stellate cell in the cerebral cortex. Stellate cells are one of the many kinds of interneurons responsible for providing cerebral cortex neurons with inhibitory input. (Scale 150:1; Drawings from [1], figure from [2].)*

2.1.3 Membrane potential

When working with neural systems the membrane potential is often a focus of study because it forms the basis of neural behaviour. The membrane potential is defined as the difference in electrical potential between the intracellular environment and the extracellular medium. In the absence of any stimulus the potential in the interior of the neuron is on average about $-70mV$ relative to the medium surrounding the neuron, conventionally defined to be $0mV$. In this state, the neuron is considered polarised. Certain molecules that span the neuron's membrane, called ion pumps, maintain the concentration gradients that cause this membrane potential difference by actively transferring ions across the cell's membrane. Thus, sodium has a higher concentration outside a neuron and potassium is more concentrated inside the cell. In this way, ions flow into and out of the neuron in response to both voltage and ion concentration

gradients. The process of positively charged ions exiting, or negatively charged ions entering, the cell through open ion channels thus making the membrane potential more negative, is known as hyperpolarisation. The opposite process, which would make the membrane potential less negative and even positive is called depolarisation [3].

2.1.4 Action potentials

When the neuron is depolarised and if the membrane potential is raised above a certain threshold value, a positive feedback process begins which ends with the neuron generating an action potential or spike. An action potential is a strong fluctuation in the membrane potential, typically of a magnitude of $100mV$ (see Figure 2.2), which lasts for about $1ms$. The action potential can be recorded at various points in the neuron's anatomy, changing only in shape (see Figure 2.2). Timing, which is considered the most important aspect of the action potential, is preserved regardless of the differences in recording location [3].

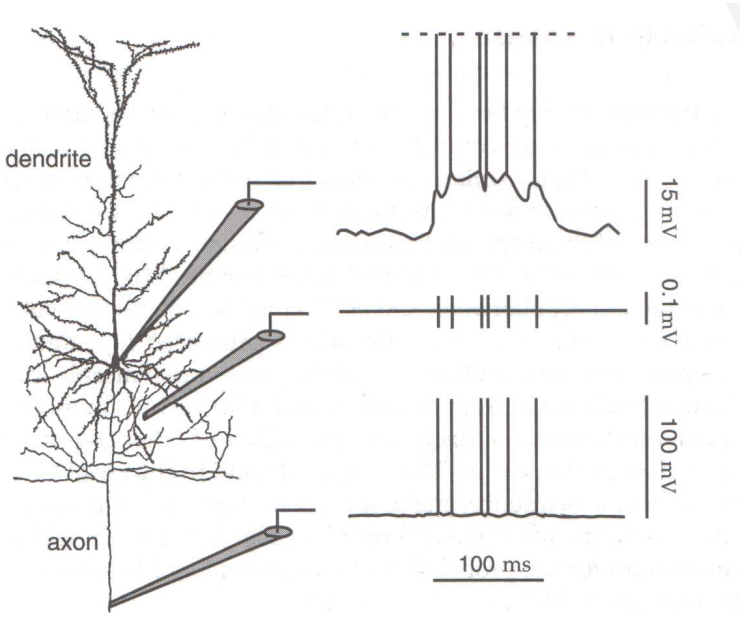

Figure 2.2: *Simulated recordings from various parts of a neuron's anatomy. The top trace represents a recording from the neuron's soma. The bottom trace represents a recording from the neuron's axon. This trace shows the full height of the action potential. The middle trace represents an extracellular recording of the action potential. Outside the cell, the amplitude of the action potential is 1000 times smaller than when recorded inside the cell. (The neuron diagram is the same as in figure 2.1A, figure from [3].)*

2.1.5 Refractory period

The ability to generate action potentials also depends on the neuron's recent activity. After firing a spike and for a few milliseconds, it is virtually physiologically impossible for the neuron to initiate the process that would generate another one. This small time period is called the absolute refractory period. After this period and for a slightly longer time interval that can last up to tens of milliseconds, it is more difficult for the neuron to fire again. This longer interval is called relative refractory period [3].

Action potentials are a fascinating and important feature of neurophysiological behaviour. The reason for that being that they are the only form of membrane potential fluctuation that can travel over large distances, quickly and with no reduction in intensity.

2.2 Recording neural responses

Recording neural behaviour is a crucial part of studying neural systems. There is a variety of methods for recording neural activity and it can also be recorded from various locations in or around the neuron (see Figure 2.2).

2.2.1 Sharp and patch electrodes

The membrane potential can be measured intracellularly using a sharp hollow glass electrode filled with a conducting electrolyte inserted into the neuron. This recording is then compared to that of a reference electrode recording from the extracellular medium. Another method is to attach a similar but broader-tipped electrode to the cell's surface that will form a tight seal. The membrane beneath the electrode's tip is then broken or perforated, thus forming an electrical continuum with the cell's interior. Typical recordings of this sort show sequences of action potentials on top of more slowly changing subthreshold potentials. Intracellular recordings can also be taken from the axon and the dendrites of the neuron. However, depending on the type of the cell, they can be very difficult and rare. Recordings from the neuron's soma are far more common. The action potential sequence in a somatic and axonal recording of the same cell is identical with the only exception of the subthreshold membrane potential fluctuations which are entirely absent from the axonal recording. This serves to identify spikes and their temporal and spatial configurations as the main information carrying characteristic of a neuron's activity

since only they propagate down axons and onto other neurons [3].

2.2.2 Extracellular electrodes

Intracellular recordings are ideal for in vitro preparations of neural tissue but they can be very impractical, since they destroy the cell and are potentially ethically dubious. Fortunately, extracellular recordings can be made which are similar to intracellular recordings from an axon. Their similarity lies in that they capture the action potential sequence but not subthreshold oscillations (see Figure 2.2). In these, an electrode is placed near the neuron and does not penetrate the cell's membrane. Thus, extracellular recordings are ideal for in vivo experiments, particularly when recording from behaving animals [3].

2.3 Neural response

Spikes do not vary enough in size, duration or shape and are normally treated as identical events in studies of neural encoding. This leads to the logical conclusion that they convey information through their timing. During a trial, starting at time 0 and ending at time T, in which the spikes are recorded, the duration of the spikes is ignored. Consequently, the spike sequence can be represented as a list of spiking times [9].

2.3.1 Firing rates

Because of a certain amount of variability in neuronal responses from trial to trial, spike sequences are usually studied under a statistic or probabilistic light. This gives rise to the term firing rate. The simplest measure that falls under this general term is the spike-count rate. This is determined by counting the number of spikes (n) that occur during a trial and then dividing by the length of the trial (T). Thus, the spike-count rate is defined as

$$r = \frac{n}{T}. \tag{2.1}$$

This measure requires only one trial to be calculated but its drawback is that all detail about the temporal evolution of fluctuations in the neural response is lost. A way to overcome this is by calculating a time-dependent firing rate by counting spikes in shorter time intervals. The

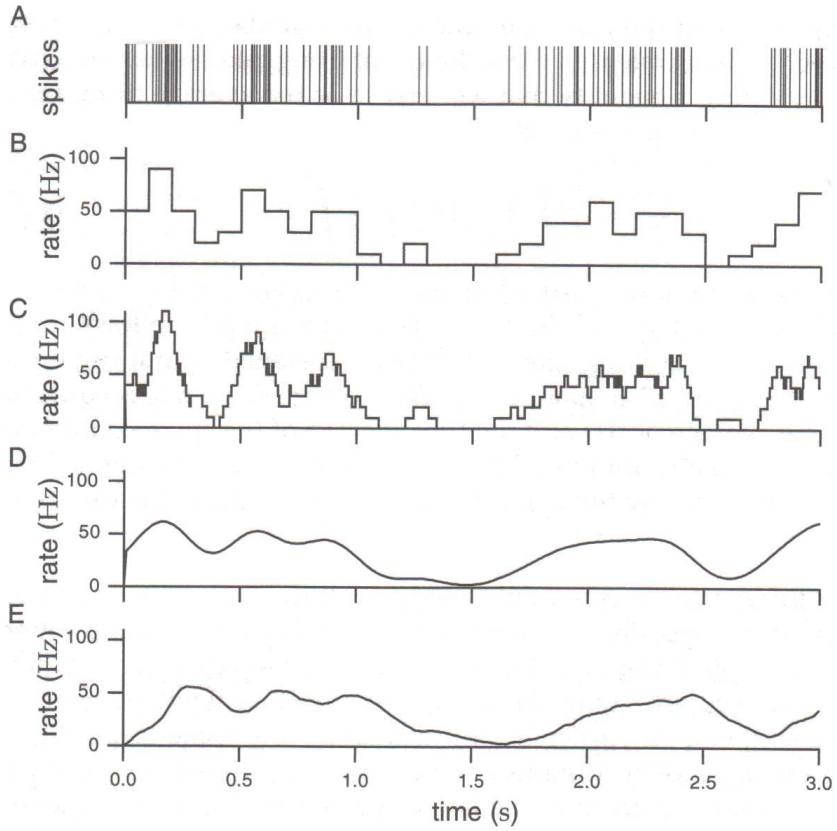

Figure 2.3: *Various firing rate approximation methods. A) A neural response. B) Discrete-time firing rate with a bin length of 100ms. C) Firing rate approximation with a sliding window with length 100ms. D) Approximate firing rate using a Gaussian window function with $\sigma_t = 100$ms. E) Approximate firing rate obtained using an α function with $1/\alpha = 100$ms. (figure from [3].)*

same principle as above can be used to obtain the firing rate at time t, however, the smaller the time interval, the higher the temporal resolution. This means that for very small intervals the firing rate will be either 0 or 1. In order to avoid this loss of measure resolution we can average over multiple trials. Consequently, the time-dependent firing rate, or $r(t)$, is the number of spikes averaged over trials that appear in a short time interval divided by the duration of the interval [9].

The firing-rate is a very useful measure in the study of neurons and neural systems. One thing about this quantity that must be kept in mind is that the time intervals over which spikes are counted, must be long enough so that there are enough spikes in them for a reliable estimate to be made. For a time interval whose length Δt is sufficiently small, the firing rate $r(t)$ times

the interval length Δt is the average number of spikes over trials in that interval. If Δt is small enough, it will never include more than one spike on any given trial. Consequently, $r(t)\Delta t$ becomes the fraction of trials in which a spike occurred in that time interval. This also means that $r(t)\Delta t$ is the probability of a spike occurring in that time interval [9].

Averaging the response over trials gives the firing rate. In a similar fashion, averaging the spike-count firing rate over trials gives us a measure that can be referred to as the average firing rate, is denoted by $\langle r \rangle$ and is defined as

$$\langle r \rangle = \frac{\langle n \rangle}{T}, \tag{2.2}$$

where n and T are the same as in equation 2.1 [9].

2.3.2 Measuring firing rates

The firing rate can be accurately, but not exactly, determined from a finite number of trials. However, there is no unique way to achieve this and various different methods of approximation are used. The simplest approach to estimating the firing rate of a spike train is to divide the neural response in time intervals or bins of equal length, count the number of spikes in each bin and then divide by the length of the interval. By changing the length of the intervals one can achieve a balance or trade-off between temporal resolution and firing rate accuracy. One way to avoid this trade-off is to use bins of variable length so that the firing rate is approximated in every time interval by a fixed number of spikes. It needs to be pointed out that in the method described above the placement of bins or time windows is arbitrary. This arbitrariness can be overcome by the use of a sliding time window of set length which also appears to provide an estimate of the firing rate with better temporal resolution. However, it is necessary to remember that rate estimates less than the width of this time window away from each other are correlated since they are estimated using some of the same spikes. The sliding window can be a function of any kind, referred to as the window function and when multiplied with the neural response function it is formally termed a linear filter. The window function is also called the filter kernel and dictates how the neural response contributes to the firing rate estimation at any point in time [9].

2.3.3 Spike-train statistics and variability

The response of a neuron typically depends on any number of characteristics and properties of the stimulus with which it is presented. The average firing rate as a function of any one of these characteristics or properties of the stimulus is called the neural response's tuning curve. Estimating the average firing rate is easy using a tuning curve but they are not adequate for understanding how the spike-count firing rate varies over trials. This is because of response variability both in terms of spike counts and in terms of temporal differences. Response variability is an important aspect of neural systems and a strong theme in this work and will be the subject of further detailed discussion [9].

Because of the variability of the neural response it is pointless to try and define the probability of a spike occurring at a specific time. Rather, it makes more sense to ask what is the probability of a spike happening inside a specific time interval of length Δt. If Δt is small enough, the probability of a spike occurring within the interval is proportional to the interval's length. The same is true for any stochastic, continuous variable. In a neural system with stochastic, continuous characteristics, the number of possible neural responses is normally so large that determining them, or even trying to estimate their probabilities, is intractable. Fortunately, we can build statistical models that allow us to estimate the probability of any possible neural response based on our knowledge of recorded spike sequences. Firing rates can determine the probability of single spikes occurring in a small time window but when it comes to more than one spikes, the probability of their sequence is not necessarily the same as the product of their individual probabilities. This is due to the fact that spikes are not always independent and uncorrelated events [30–33].

A stochastic process whose output is a series of events is termed a point process. Neurons can be considered to be point processes since they are stochastic and neural activity can be considered a series of events. The probability of any one event at any point in the event sequence can depend on the entire history of preceding events in the sequence. If the event probability depends only on the previous event, thus making intervals between events independent, the stochastic process is called a renewal process. If on the other hand, the events are statistically independent from each other, the process is called a Poisson process. A Poisson process is an extremely appropriate approximation of the process of neural activity [30–33].

A useful measure for studying and characterising spike sequences is the interspike interval

distribution. This is the probability density of time intervals between neighbouring spikes. For a Poisson process the interspike interval is an exponential (see Figure 2.4). This means that short interspike intervals are more likely than long ones.

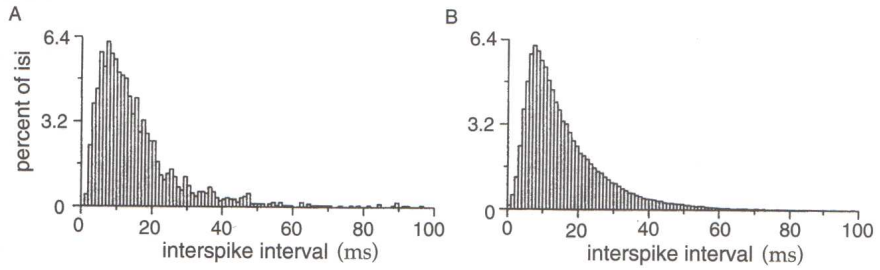

Figure 2.4: *A) The interspike interval distribution from a medial temporal neuron responding to a moving, random-dot image. The percentage of interspike intervals falling into each bin is plotted against interspike interval length. B) The interspike interval histogram of a Poisson model with a stochastic refractory period. (figure from [3] an adaptation from [4].)*

Using the interspike interval distribution of the Poisson process (see Figure 2.4) we can determine the mean interspike interval and the variance of interspike intervals. The ratio of the standard deviation σ_τ to the mean interspike interval τ is called the coefficient of variation

$$C_V = \frac{\sigma_\tau}{\langle \tau \rangle}. \tag{2.3}$$

The interspike interval distribution is only useful for measuring the distribution of times between adjacent spikes in a spike train. Therefore, it is necessary to generalise this notion and measure the distribution of times between any pair of spikes in the neural response. This new concept is called the autocorrelation function and it is very useful for detecting patterns in spike trains, such as oscillations [9].

In the same way, we can generalise even further and correlate pairs of spikes from the spike trains of two different neurons by determining the distribution of time intervals between them. This measure is useful for uncovering phenomena such as synchronised firing, or asynchronous but phase-locked firing, between pairs of neurons. It also provides a link to statistical and analytical measures that will be explained in detail in further chapters. The Poisson process can describe a great amount of recorded neural data but not all of it. There are still mechanisms and phenomena that cannot be explained by the Poisson model and its statistics.

2.4 The neural code

When studying neural systems, regardless of one's point of view, whether electrophysiologist or computational neuroscientist, certain terms such as code or information need to be used. But what does it mean for a neuron or an entire population of neurons to convey information? Are neurons using a specific scheme for doing this? Are they using more than one way to convey information about themselves and their surroundings? These questions are at the core of neuroscience. It is obvious that neural systems must use specific schemes in order to transmit information and understand it. However, there is still a lot of debate as to what those schemes are exactly. Is information encoded in every single action potential? Can a single neuron convey enough information about a specific stimulus? Certain researchers feel that these questions are central to understanding how neural systems work. It could be the case that neurons on their own are incapable of conveying enough information to perform all the important tasks at hand. Another important focus of debate in this area of research is whether neurons use a rate code or a temporal code. The answers to the above questions are fundamental for our understanding of the intricate workings of the neural system.

2.4.1 Independent spike code

If the spikes in the neural response can be described by an inhomogeneous Poisson process, the time-dependent firing rate contains all the information about the stimulus that can be conveyed by the neural response. In this case, the code used by the neural system can be termed as an independent-spike code. This definition points to the fact that in this case the generation of an action potential is independent of all the other spikes in the neural response [9].

2.4.2 Correlation code

In contrast to that, if spikes do not encode information independently of each other, the neural code can be said to be a correlation code since information can also be encoded in correlations between spikes. What probably happens in reality is that the neural system encodes information in both independent spikes and correlations of spikes. Consequently, any dividing line drawn in order to try and characterise the code as an independent-spike code or a correlation code, is arbitrary. However, such a distinction is necessary. It is usually achieved by characterising an encoding scheme as a correlation code if a significant amount of information is conveyed

by correlations, comparable to the amount conveyed by individual, independent spikes. An example of a correlation code is one that would convey a significant amount of information in interspike intervals. However, information could be encoded in more complex correlations of spikes [9, 30–35].

Overall, an independent-spike code is much simpler to study and analyse than a correlation code. Most research in neural coding is based on the assumption that spikes are independent. This is backed by the fact that even though some information has been found to be carried by correlations in spikes, it is not a terribly significant proportion when compared to the amount of information carried by independent spikes. It is possible that there still remain correlations that we are unaware of which could be very significant in terms of neural coding. However, it seems unlikely and based on fairly convincing evidence, independent-spike coding can at least be deemed as an adequate approximation [9, 30].

2.4.3 Independent neuron code

So far, we have discussed the ways in which a neuron can convey information, but information in the nervous system is typically handled by populations of neurons. This means that when studying neural population coding we need to know whether neurons process information independently from each other or whether information is carried in correlations between their responses. Typically, it is assumed that the response of every neuron in the population studied is statistically independent and this is referred to as independent-neuron coding. Notionally, this does not mean that neural responses in the population are not combined into a whole. It means that they can be combined without taking correlations between spikes into consideration [9, 30]. In this case, the whole is not greater than the sum of its parts. This is an assumption that requires validation in each case by asking whether any additional information is provided by the correlations between neural responses that cannot be provided by the neural responses considered individually.

2.4.4 Synchrony and oscillations

A population correlation code could potentially have a variety of mechanisms for conveying information. One of these is synchrony. Rhythmic oscillations of neuronal population activity are another possible mechanism. Both synchrony and oscillations are common characteristics

of neural activity. However, their existence is not adequate for supporting the existence of a correlation unless it can be proven that they convey an amount of information comparable to that explained by the independent-neuron coding hypothesis.

2.4.5 Temporal codes

In the cases where it can be found that a significant amount of information about the stimulus is encoded using precise spike timing or high-frequency firing-rate fluctuations, the neural code can be termed a temporal code. The neural response, and particularly its temporal aspect, is the direct result of the nature and dynamics of the stimulus and the encoding mechanism of the neural system. Typically, rapidly changing signals result in precisely timed spikes in the neural response and corresponding changes in the firing rate regardless of the neural code employed. What ultimately leads to the characterisation of a neural code as temporal is the fact that temporal precision in the neural response arises from the properties of the stimulus [9, 30, 31, 33].

A useful way to distinguish between rate and temporal coding is by observing the behaviour of the firing rate. If the firing rate varies slowly over time, the code is typically called a rate code and if it varies rapidly it is called temporal. However, this is an ambiguous, almost arbitrary distinction. What criterion do we use to identify the firing rate as a slowly or rapidly changing one? One approach is to observe the coincidence of firing rate peaks and spikes. This coincidence could mean that the change in firing is due to that particular spike or at most a few spikes in the neural response. This possibility is intuitively correct but cannot be extended and applied in the framework of population coding since many spikes can be produced before a change in the population's firing rate. This leads to the paradoxical conclusion that even though a neuron can use a temporal code, the neural population it belongs to may not be able to. Another approach is to study the stimulus in order to determine whether a temporal code is used. In this case, the code is termed a temporal one if information is conveyed by characteristics of spike timing in the neural response that happen in a shorter time-scale than the fastest fluctuation of the stimulus. This approach based on the stimulus, disqualifies as temporal code candidates, many cases in which a temporal code was reported on the basis of spikes [9].

There is still debate about the nature of neural coding, whether it is rate or temporal, and identifying the temporal nature of any neural response is of critical importance. However, when studying neural activity, especially in a population, one needs to identify and study the

relationships between neurons and their responses.

2.5 Modelling neurons

Much is known about the biophysics of neural activity and based on this knowledge models of neurons can be built. Over the years many models have been formulated ranging from the biologically accurate and computationally costly to the greatly simplified but highly efficient. Chosing one is a matter of convenience and efficiency.

2.5.1 Levels of modelling

Deciding which point to pick in this spectrum of neuron models is a choice that must be made while keeping in mind the experimental basis and the goals of the research at hand. There are certain forms of complexity when modelling neurons that a researcher must take into account. The combined effect of biochemical properties is one of those and it is one of the causes for the variety of neural dynamics that have been observed so far. The other is the morphology of the neuron which plays an important part in receiving, integrating and transmitting information. Choosing an overly simplistic model can be used to study neural populations of great size without paying attention to the particular intricacies of each cell at the risk of giving inaccurate results. On the other hand, more biologically accurate models can help study the underlying mechanisms of neural activity in great detail while at the same time risking drowning interesting results in essentially useless complexity [3].

Neuronal models that describe the membrane potential of a neuron using a single variable, typically V, are called single-compartment models. In contrast to this kind of model, multi-compartment models elaborate on the morphology of the neuron and typically include spatial, in addition to temporal, variations in the membrane potential [3]. For the purposes of this work, single compartment neuron models were used, simply because they are more computationally efficient and complex neuron morphology was not within the scope of this line of research.

2.5.2 Voltage dependent conductances

The basic notion that is expressed through the equations defining single-compartment models is that charges flow into and out of the neuron thus changing its membrane potential. The equation

that describes this underlying notion is

$$C_m \frac{dV}{dt} = \frac{dQ}{dt}, \tag{2.4}$$

and it is the notional foundation of any kind of single-compartment model. What this equation describes is the proportional relationship between the rate of change of the membrane potential and the rate of charge build-up in the neuron. The rate at which charge builds up in the neuron is equal to the total current entering the cell which is the sum result of all membrane, synaptic conductances and any current injected into the neuron. This notion leads to the reformulation of the above equation into

$$c_m \frac{dV}{dt} = -i_m + \frac{I_e}{A}. \tag{2.5}$$

where i_m is the membrane current and is defined as positive-outward, I_e is current that enters the neuron through an electrode and is defined as positive-inward and A is the surface area of the neuron. This is the basic equation for all single-compartment models [3].

The underlying cause of most interesting characteristics of neural activity is active membrane conductances. Research has shown that single channels which allow current into and out of the cell, open and close rapidly and in a stochastic manner. Thus, neuron models must describe how the probability of a channel being open or closed is affected by the membrane potential. Most neuron models describe channel dynamics in a deterministic fashion which is a justified approximation if one takes into account the fact that ion channels form extremely large populations on the neuron's surface. Thus, from the law of large numbers, the probability that any one channel is open or closed at any one time is approximately equal to the fraction of channels that are in the same state in the population [3].

2.5.2.1 Channel gates

Channels come in two different types, those that produce a persistent conductance and those that produce a transient one. Channels are complex molecules that permeate the cell's membrane and their gating mechanisms involve complex conformational changes in the molecule's structure [3]. However, for the purpose of simplicity, most of the time the are depicted as structures with swinging gates attached to voltage sensors that allow them to open or close (see Figure 2.5).

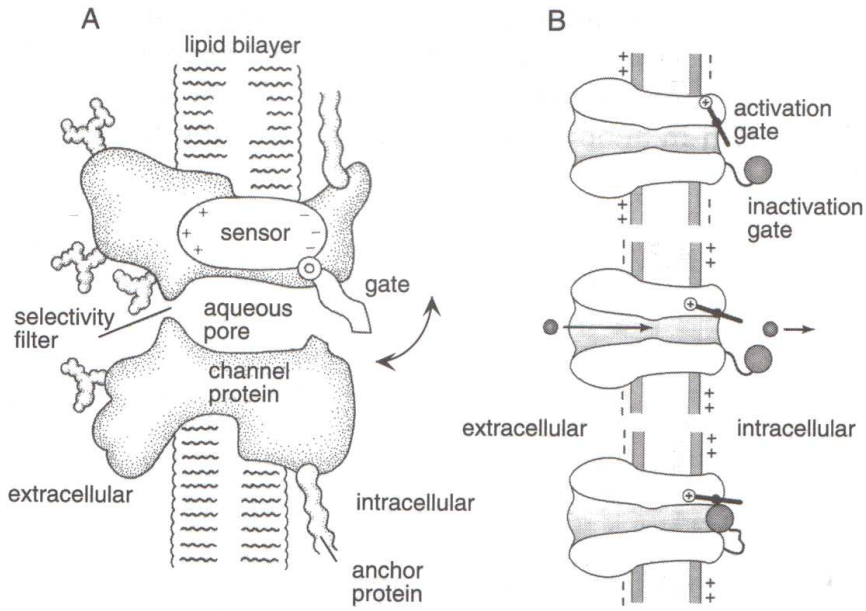

Figure 2.5: *Membrane Channel gating. A) Gating of a persistent conductance. The gate is opened and closed by a sensor that is sensitive to the membrane potential. The channel has a selectivity filter that allows only ions of a specific kind to pass through. B) Gating of a transient conductance. In this case too, the activation gate is coupled to a voltage sensitive sensor. However, in this case there is a second gate which can block the channel once it is open. The top shows the channel in a deactivated state, the middle in an activated state and the bottom in an inactivated state. Only the middle state is an ion-conducting state. (A from [5], B from [6].)*

2.5.2.2 Activation

Channels can have a number of different types of gate. Those that act as if they had only one type of gate produce what is said to be a persistent or noninactivating conductance. The opening of this gate is called activation of the conductance and closing the gate is called deactivation. As for all channels, the probability of the channel's gate being open or closed depends on the neuron's voltage. When the cell is depolarised, the probability that the gate is open increases and when the cell is hyperpolarised it decreases. An example of such a channel is the K^+ channel which is responsible for repolarising a neuron after it has fired an action potential [3].

As mentioned above, all channels undergo changes in their conformation in order to open and produce a conductance. In the case of the K^+ channel, each gate is made up of four identical

subunits and all four must change their conformation for the channel to open. The probability of the channel gate being open can then be expressed as n^k where k is the number of independent, identical events, that is subunits undergoing conformational changes, that need to happen for the channel to open and n is the probability that any one of the subunits has undergone those changes. In this case, n is called an activation variable and describing its mechanism of dependence on voltage and time is to describe the conductance itself [3].

Channels with more than one type of gate and therefore more than one gating processes, only open momentarily, or transiently, when the neuron is depolarised. In this case, there will be a number of variables controlling the conductance produced by the channel equal to the number of gating processes. Using the example of the Na^+ transient channel, m is an activation variable similar to that of the K^+ channel, n. However, this channel has an additional blocking mechanism described by a variable h, also known as the inactivation variable. The activation variable m is distinguished from the inactivation variable h by the fact that m increases when the neuron is depolarised and decreases when it is hyperpolarised whereas h decreases during depolarisation and increases during hyperpolarisation. As for the K^+ channel, the probability for the Na^+ channel to be open at any time is $(m^k)h$ [3].

2.5.2.3 Channel kinetics

The mechanisms underlying the transitions of channels and their subunits from open to closed are collectively termed channel kinetics. In the case of the K^+ channel and its subunits, they are formally described by a kinetic scheme in which the transition from closed to open happens with a voltage-dependent rate of $\alpha_n(V)$ and the reverse transition, from open to closed, with a voltage-dependent rate of $\beta_n(V)$. The probability that a subunit of this channel opens is equal to the product of the probability of finding the gate subunit closed, $1 - n$, and the opening rate $\alpha_n(V)$. In similar fashion, the probability of the subunit closing is equal to the probability of the subunit being open, n, times the closing rate $\beta_n(V)$. This leads to a formal definition of the rate with which the open probability for a gate subunit changes states

$$\frac{dn}{dt} = \alpha_n(V)(1 - n) - \beta_n(V)n. \tag{2.6}$$

Therefore, it becomes clear that the important factors in determining n are the opening and closing rate functions $\alpha_n(V)$ and $\beta_n(V)$. These functions can be determined by fitting electrophysiological data [3].

The same is true for gating variables m and h of the transient Na^+ channel. They too are governed by opening and closing rates which need to be determined in order to accurately describe the opening and closing mechanisms of the channel. The only difference in this case is the fact that increase in m is called activation and decrease is deactivation and, to distinguish between the two variables, increase in h is called inactivation whereas decrease is called deinactivation. All of the above hints to the fact that in order for the Na^+ channel to conduct, both gating variables must be non-zero [3].

2.5.3 Hodgkin-Huxley model

The Hodgkin-Huxley (HH) neuron model is one of the first models to be constructed and in its simplest form its membrane current is made up of the sum of voltage dependent currents

$$i_m = \bar{g}_L(V - E_L) + \bar{g}_K n^4(V - E_K) + \bar{g}_N a m^3 h(V - E_N a), \tag{2.7}$$

where $\bar{g}$ denotes a maximal conductance and E a reversal potential. In its entirety, the model comprises of the basic equation for all single-compartment neuron models combined with the equation for the membrane current and voltage-dependent gating variable equations as those described above [3]. The dynamics of these variables over time and during an action potential can be seen in Figure 2.6. These equations can also be used to build models with more than one compartment for the purposes of modelling neurons with more intricate morphologies. This is a detailed model which puts weight on biologically accurate reconstruction of neural activity. This makes it an ideal candidate for studies of neural activity where a high degree of biological plausibility is of paramount importance. However, for research that is focused on the behaviour of larger groups of neurons, the HH model is not a viable choice since it is computationally demanding [3].

2.5.4 Integrate and fire model

To circumvent the obstacle of increased computational costs we can use neuron models which do not describe action potential generating mechanisms explicitly but capture the overall behaviour. The Integrate-and-Fire (IF) model is just such a model. It describes the action potential generation behaviour of the neuron simplistically. This means that a spike is generated whenever the membrane potential reaches a specific threshold value and then it is reset to a value

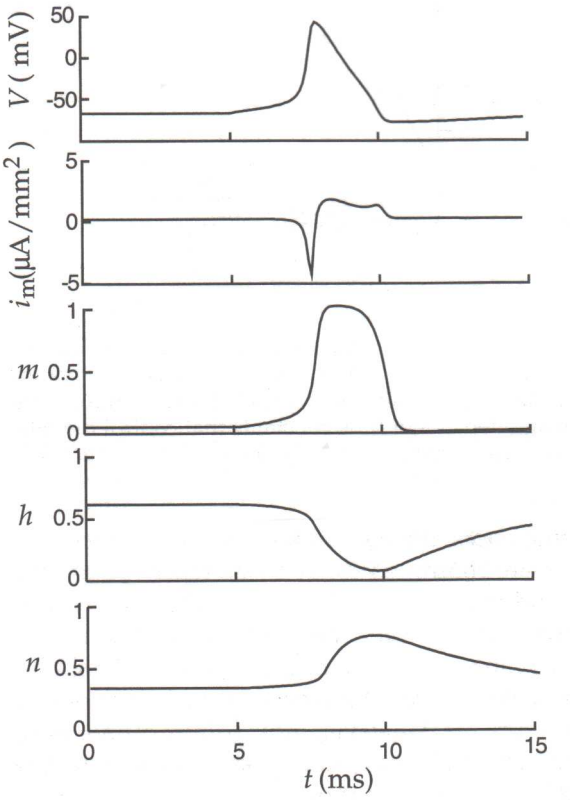

Figure 2.6: *Dynamics of the variables m, h and n governing channel kinetics, the membrane potential V and membrane current i_m during an action potential. Current injection was initiated at $t = 5$ms. (figure from [3].)*

below the threshold potential. This model is quite old, it pre-dates our understanding of the underlying mechanisms of action potential generation but despite this, it is still a very useful description of neural activity. The basic equation that describes it is the same as that which describes all single-compartment models

$$c_m \frac{dV}{dt} = -\bar{g}_L(V - E_L) + \frac{I_e}{A}, \tag{2.8}$$

with all parameters as defined previously, together with a rule that fires a spike whenever the membrane potential reaches a specific threshold value and then resets the membrane potential to a subthreshold value [3].

The IF model can also be improved upon and it can be given properties such as spike rate adaptation and refractoriness which are important when studying neural activity. It can also

be granted more elaborate neurocomputational features and characteristics but then it starts resembling the Hodgkin-Huxley model both in form and in computational cost. Consequently, at least for the purposes of this work, a neuron model is needed that has comparable computational efficiency to the IF model but also a certain degree of biological plausibility and detail similar to that of the HH model [3].

2.5.5 Izhikevich model

Using bifurcation methodologies one can reduce the dimensionality of complex, biologically accurate neuron models, such as the Hodgkin-Huxley model, while at the same time allowing them to maintain the neural activity characteristics that make them realistic [36]. In particular, there is a specific neuron model, called the Izhikevich neuron model, which sits between the Hodgkin-Huxley model and the Integrate-and-Fire model in terms of biological plausibility and computational efficiency [7, 37]. It is a two-dimensional model of a neuron with barely a few more computations per time step than the Integrate-and-Fire model that reproduces faithfully a great variety of neurocomputational features displayed by real neurons [37].

It is a particularly versatile model and allows for a variety of neural behaviours and flexibility

$$\begin{aligned} v' &= 0.04v^2 + 5v + 140 - u + I \\ u' &= a(bv - u) \\ if\ v \geq 30mV\ then\ v \leftarrow c,\ u \leftarrow u + d. \end{aligned} \tag{2.9}$$

By tuning the parameters a, b, c and d one can control the time scale of the recovery variable u, the resting potential, the reset value of the membrane potential v after a spike has been fired and the reset value of recovery variable u after spike generation respectively [7]. In this set of equations as well as in all that follow the ”prime” diacritic signifies the difference between the new and the old value of the parameter (eg. $v' = v_{new} - v_{old}$).

This model displays an impressive array of neurocomputational features simply by tuning the above parameters. Post-inhibitory rebound, bursting, chattering, subthreshold oscillations and regular or fast spiking are only a few of the possible real behaviours this neuron model can replicate accurately [37]. Because of this ability to accurately approximate a great variety of neural behaviours and the fact that it scarcely costs more in terms of computation than one of the

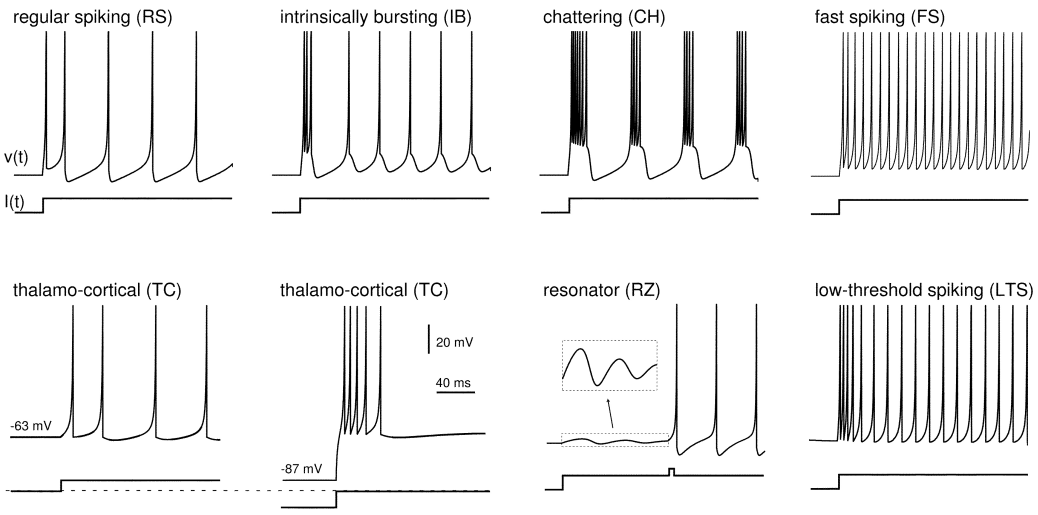

Figure 2.7: *A few examples from a variety of neurocomputational features that the Izhikevich spiking neuron model demonstrates. (Adapted from [7].)*

lightest neuron models ever designed [37], the Izhikevich neuron model is an ideal candidate for research whose focus is neural populations and in which a certain degree of biological plausibility is not only fortunate but also desirable.

2.6 Neural networks

Typically, a neuron in the mammalian neocortex receives several thousands of inputs via synaptic connections. This is the defining characteristic for a neural network, connectivity. Synapses are what connects neurons in a neural population and it is widely believed to be what grants neural systems their impressive computational and analytical capabilities. Neurons are an impressive type of cell but ultimately they are not capable of any complex behaviour at least in terms of computation. To elucidate the mysteries of neural computation, to understand what makes brains work, we need to study interconnected neural populations, otherwise referred to as neural networks [3].

2.6.1 Connectivity

When studying neural systems one invariably looks for inspiration in real, biological instances of neural networks. One of the main issues that arise when building and studying a neural net-

work is the nature of its structure. In certain cases of biological neural networks there are explicit hierarchies in how the structure is arranged, with layers of neurons receiving inputs from those of the layers below them and sending signals to layers of neurons above them [38]. This intuitively points at a combinational aspect of computation where information is processed, combined and then passed on to higher levels of processing. Networks that process information in this straightforward way, in a single direction, are also known as feedforward networks. In all of the experiments that follow, the neural populations are feedforward neural networks unless otherwise stated. Also, the neurons are only excitatory. This choice was made for simplicity's sake and was backed by some preliminary results of experiments which included inhibitory neurons. The qualitative characteristics of stochastic behaviour did not change with the addition of inhibition but it was left out as an unecessary complication. Additionally, all synaptic connections in the neural populations used in this work are time-delayed. The time-delays are uniformly distributed between 1 and $4ms$. Connectivity in all the neural populations that are used in this work is 20% for all kinds of connections, feedforward, lateral and recurrent. The connection weights are uniformly distributed from 0 to 20.

However, this is certainly not the only type of architecture in neural networks. Networks with the ability to feed information back to previous layers of neurons after higher levels have processed it are called recurrent neural networks. These networks demonstrate a richer variety of dynamics than feedforward networks but are also harder to study. Neurons are also typically classified as excitatory or inhibitory based on whether they excite or suppress respectively their post-synaptic targets [3].

2.6.2 Plasticity

One of the most interesting abilities of synaptic connections and consequently neural networks is their malleability. Synaptic plasticity, particularly when dependent on activity, is widely considered to be the underlying mechanism of learning and memory. It is also the driving force behind the formation of neural networks [3].

There are many ways in which neural activity can and does affect synaptic strength. One of the first and fundamental experimentally determined rules that attempted to explain the way in which neural activity drives synaptic plasticity is the Hebb rule. In the process described as Hebbian learning, if a neuron contributes to the activity of a second neuron, then the synapse connecting them ought to be strengthened, a process called potentiation. Much of the following

research into the role of synaptic plasticity in learning and memory is based on this rule. More generalised versions of this rule also predict that synaptic strength changes proportionally to the correlation between the activities of the two neurons. This means that if the first neuron fails to contribute to the second neuron's activity, synaptic strength is decreased, a process also known as depression [3].

Studying synaptic plasticity is typically carried out over the course of periods of time when changes in synaptic strength due to neuronal activity are likely to happen, namely during training or learning. There are various different learning frameworks and one such framework is unsupervised learning. In unsupervised learning, the neural network rearranges its connectivity solely as a response to the learning rule that is in effect and the nature of the input [3].

In contrast to that, supervised learning is a guided learning paradigm. A certain expectation is imposed on the network, that of reproducing the relationship between a specific set of input and output. This is a less biologically plausible framework but one that produces networks trained to perform specific tasks [3].

A more biologically plausible form of learning is reinforcement learning. In this framework, one network acts as the teacher of a second network not by imposing an expectation but by providing evaluation and feedback based on a reward scheme. Reinforcement learning is a particularly useful paradigm especially when the nature of the relationship between input and output is unknown [3].

In addition to activity dependent learning rules there are also timing dependent ones which are even more biologically plausible. Spike-timing-dependent plasticity is a framework within which synapses are potentiated when the generation of a spike in the pre-synaptic neuron preceded a spike in the post-synaptic one. Conversely, if the pre-synaptic neuron fires after the post-synaptic one the synapse is depressed. This is clearly a learning paradigm which takes into account causality among neurons [3].

2.7 Why spiking neural networks

The most obvious reason for choosing spiking neural networks as a framework for studying phenomena and processes is that they are the most biologically relevant and plausible paradigm of artificial neural networks. However, there is another, more important reason which is not

as obvious. Spiking neural networks are widely considered to be computationally superior to either binary or analogue artificial neural networks. This means that while studying spiking neural networks not only are we more likely to understand better the workings of real, biological neural networks but it also becomes possible to analyse and create more powerful computational systems [39–45].

2.8 Summary

In this chapter, a quick overview was made of neuron anatomy and electrophysiological properties. Basic principles of the study of neural activity were presented along with the fundamental methodology for analysing it. Fundamental concepts were detailed for studying the activity of a neural population along with a brief but concise neural coding taxonomy. The fundamental principles of neural modelling were covered along with the spiking neuron model that was used in this work. A brief introduction was made about the properties of the neural populations that will be used later in this work and justification was given for all the methodological choices made so far.

Chapter 3
Noise and stochasticity

The activity of neurons, when recorded in vivo, is highly irregular. This irregularity and unreliability is called noise. Before more detailed analysis of neural behaviour and encoding was carried out, this phenomenon was considered an obstacle. Many recordings of electrophysiological data must be made in order to obtain the average behaviour over multiple, identical presentations of a stereotyped stimulus. In many cases, spikes in the neural response seem to occur spontaneously where there would be no apparent cause for them. In other cases, spikes failed to be elicited when they were expected. This phenomenon raises a certain very important question: Is noise an obstacle that the nervous system must strive to overcome or is it part of the system's information encoding scheme? This question remains, at least in part, unanswered, mainly because there can be no resolute conclusion on the role of noise in information encoding and processing in neural systems if it is not known exactly what those encoding and processing schemes are [3, 9].

Neuron models on the other hand, are very much deterministic. When presented with the same input they will produce the same response. To help understand the precise effect of noise on the processing capabilities of neural systems when using spiking neuron models, noise is usually added explicitly in order to not just achieve superficial biological plausibility but to reproduce the unpredictable nature of neural responses.

3.1 Sources of stochasticity

Ultimately, noise is a free form of energy. It permeates the environment in which neural systems exist, but also arises from the very components of these systems. When dealing with noise and its effects one has to differentiate between these two types of noise sources. Formally, these are referred to as intrinsic, when they cause stochastic behaviour on the level of individual neurons, and extrinsic, when they generate stochastic dynamics on the level of synaptic transmission, connectivity and generally larger scale network effects [46].

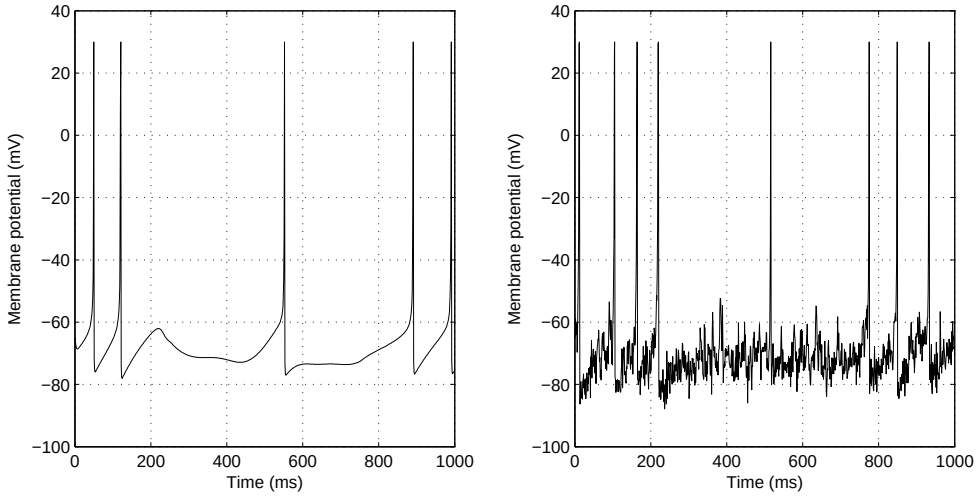

Figure 3.1: *The effect of noise on the activity of a spiking neuron. On the left, a deterministic Izhikevich neuron model with no form of stochasticity. On the right, the same model presented with an identical input signal and additive Gaussian noise. Apart from the subthreshold oscillations that have been introduced in the neuron's activity, some action potentials have been displaced, some have been added and some have been removed in comparison with the activity of the deterministic version of this model.*

3.1.1 Intrinsic noise sources

An example of a noise source that works on the level of individual neurons is caused by the finite number of ion channels on any given part of the neuron's membrane [47, 48]. The formulation of spiking neuron models is based on the assumption of a great number of channels, enough to make the probabilistic fluctuations between their two states, open and closed, easy to approximate with deterministic equations. In reality, channel conductivity fluctuates and, consequently, so does the membrane potential. In the event that the membrane potential is close to the threshold, fluctuations in the membrane potential can be potentially responsible for the generation of spikes [3].

3.1.2 Extrinsic sources

An important extrinsic noise source, that is one that generates stochasticity on the level of an entire network, is synaptic transmission. Synaptic transmission is an unreliable process and only 10 to 30 percent of pre-synaptic action potentials make it through to their post-synaptic

targets [49, 50].

The summed activity of the network is also an extrinsic source of stochasticity. A neuron is not an isolated unit. It is surrounded by thousands of other active neurons. This summed activity is a constant noise background. In some cases, for example when spike sorting, this is an obstacle because one has to find ways to separate spikes from the background noise.

Finally, a less important noise source is thermal noise, otherwise known as Johnson noise. This form of stochasticity is present throughout any and all nervous systems. However, its effects compared to those of the sources mentioned above are negligible [46].

3.2 Introducing noise in formal spiking neuron models

In order to study the effect that noise has on a single neuron and populations of neurons, one must find a way to introduce stochasticity in formal spiking neuron models. One of these methods is known as escape noise. In this approach, the neuron's firing threshold fluctuates. This model is also known as the noisy threshold model. What it amounts to is that the neuron might fire even if it has not reached the formal threshold defined and it might stay inactive after having crossed it [51].

When using the method of escape noise, stochasticity affects the model at every time step, assuming of course that the time step is small enough. If a parameter of the model is changed stochastically after every spike rather than after each time step, so that the parameter between spikes is deterministic, the process is termed as slow noise. The term slow contrasts the dynamics of the stochastic process to those of the neuron [51].

The simplest way to add stochasticity to an otherwise deterministic process such as a set of differential equations describing the dynamics of a neuron is to add a noise term to said equations. Typically, the stochastic process is Gaussian in nature with a mean of zero and it is simply added to the parameter that needs to be changed from deterministic to stochastic [51]. In this case, the stochastic parameter σ_n is added to the membrane potential of each neuron (see 2.9).

Noise also comes in a variety of shapes and colours. The probability density function of the stochastic process that is applied to the neuron model can be uniform, Gaussian, Laplace or Cauchy, to name a few. The colour or frequency content of the noise can vary as well. However, such intricacies are not within the scope of this work, mainly because they have been

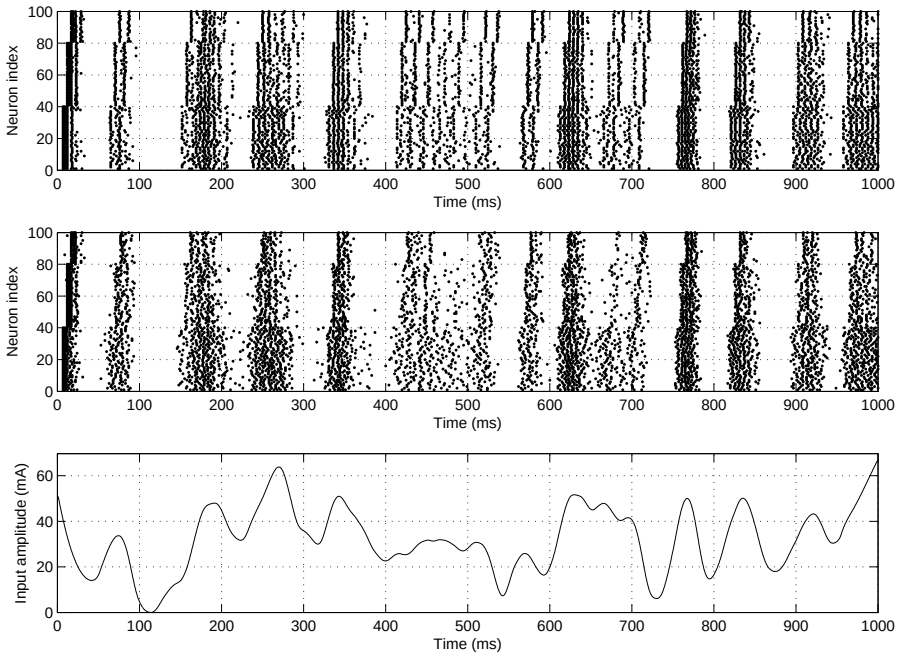

Figure 3.2: *The effect of noise on the activity of a network of spiking neurons. In the top diagram is the typical activity of a network of Izhikevich neurons without any noise. The middle diagram shows the activity of the same network with additive Gaussian noise. Although the differences are not easy to discern, a closer inspection reveals that the network's activity has changed significantly. Certain spikes have moved closer together whereas others have moved away from each other and as in the case of the individual neuron some have disappeared and some have appeared where there were none. The bottom trace shows the input signal to both versions of the network, deterministic and stochastic.*

well studied, but also because Gaussian white noise is a more than adequate approximation of stochastic behaviour [8, 12, 13].

3.3 Justification

Both the nature of the stochastic process and its probability density function have been chosen with two things in mind: simplicity and plausibility. Additive Gaussian white noise is a very simple, yet biologically relevant way to introduce stochasticity in the Izhikevich neuron model. This guarantees that any results obtained due to stochastic phenomena can be generalised. It also means that conclusions could be drawn about biological neural networks [8, 12, 13].

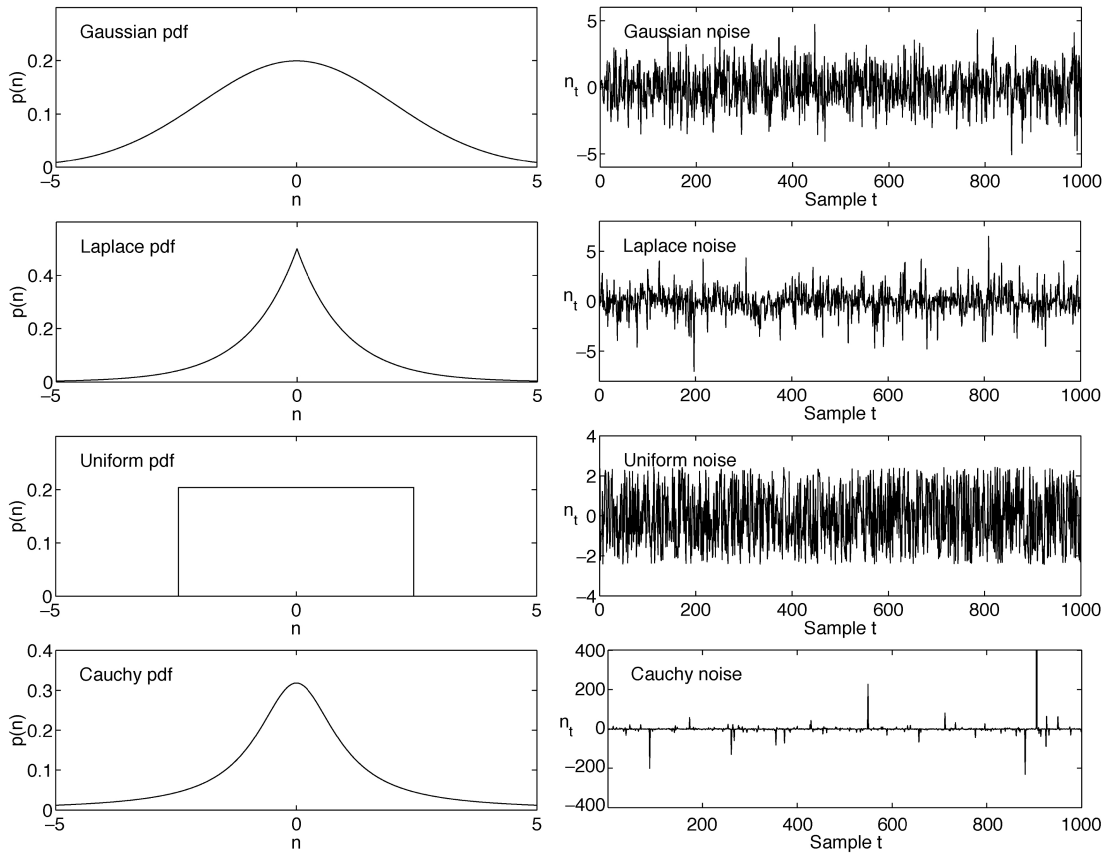

Figure 3.3: *Four characteristic examples of different kinds of noise. The top two traces show the probability density function and a sample of Gaussian noise. The second pair from the top show those of Laplace noise. The second pair from the bottom show the probability density function and a sample of uniform noise. The two traces at the bottom show those of Cauchy noise. (figure from [8].)*

Understanding how stochasticity can optimise a neural population's performance in terms of information transmission and processing can lead to a greater understanding of how biological neural networks take advantage of their surrounding and intrinsic stochasticity.

3.4 Effects of noise

There is a variety of phenomena due to noise in neural networks, some have been studied extensively and some may not be fully understood yet. There is also the possibility that many are yet to be discovered. Neurons are simple computational units that are organised into complex and

powerful computational ensembles. However, they are quite unreliable and being part of large populations only adds to their surrounding noise. Phenomena that arise from these properties and mechanisms have been, and still are, the focus of many researchers [10–26].

3.4.1 Stochastic resonance

In terms of information transmission, there is a certain phenomenon due to noise that has been well studied and is well known. When a neuron is presented with subthreshold input it does not fire and consequently transmits no information. It was observed that in the presence of some noise action potentials do occur and therefore information about the input is transmitted. On the other hand, too much added noise causes the neuron to fire at a constant rate and mostly in response to the noise itself rather than the input. This too translates to transmitting very little information about the input. Therefore, there must be a non-zero noise amplitude somewhere in the middle, an optimum that is, for which information transmission about the input is maximised. This phenomenon is known as Stochastic Resonance (SR) and it is very well documented and studied in a variety of contexts [10–15].

At first glance, this is a counter-intuitive observation, contrasting our notion of noise as an obstacle that needs to be overcome or removed. However, this phenomenon allows the detection of weak signals, something which can be of extreme importance in certain contexts. It can also be shown to be the basis of more complex information dynamics inside a neural population. Neural networks have evolved in an environment that is inherently noisy and are themselves unreliable computational units. They may have evolved to be taking advantage of this permeating stochasticity in order to improve their information transmission and their information processing capabilities. In fact, there is substantial evidence that noise may not only be beneficial but also necessary for optimal information transmission and processing in a neural population [9].

It is also necessary to understand the relevance of this to biological neural networks. The same phenomenon due to noise can be observed in the central nervous system on a scale that was previously not known. Clearly, this is the basis of a new field of research in which the effect of noise has ceased to be a negative one. It is slowly becoming apparent that noise may not just be beneficial. Stochasticity is quickly becoming essential for an adequate explanation of the mechanisms underlying information transmission and processing [15].

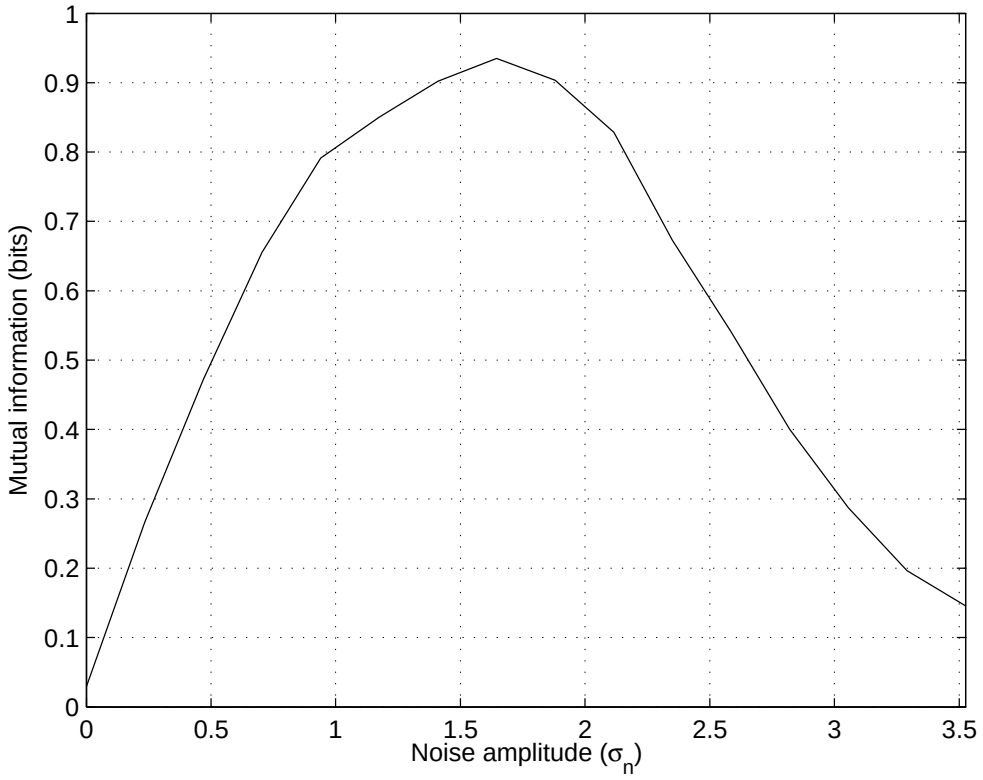

Figure 3.4: *The characteristic signature of SR. In this example, an individual neuron model's mutual information, measured in bits, between its input and output is plotted against the amplitude of the additive Gaussian noise. The neuron is an Izhikevich spiking neuron model and the noise is added to its membrane potential.*

3.4.2 Coherence resonance

In the case of SR, additional noise enhances the neuron's response to subthreshold input. However, noise can also be shown to improve the regularity of periodic components in the behaviour of the neuron or a population of neurons. This phenomenon is called coherence resonance and it is merely an extension to SR, often termed autonomous stochastic resonance [52].

3.4.3 Encoding

As mentioned above, SR is a simple phenomenon which could potentially form the basis of a new field of research in neural computation. The most obvious criticism one could make about

the use of such a phenomenon is that simply because information transmission is maximised, it does not mean that the neuron or network has become a more powerful information processing system. After all, there is a reason neurons have thresholds and that is so that they can function as filters, leaving out background activity and input that could potentially be irrelevant to them. This means we must build and elaborate upon concepts such as SR in order to obtain concrete evidence about the potentially positive effects of noise on aspects of neural networks such as encoding, plasticity and information processing.

It is well known that neural responses are highly variable depending on the nature of the input received by the neuron. The more constant and unvarying the input the less reliable the neural response. Contrary to intuition, neural responses become more reliable as the temporal nature of the input signal becomes richer [48, 53]. Intuitively, noise affects the way time-varying input is encoded but in an unexpected way. There is also evidence that noise may improve encoding of slowly varying stimuli whereas it appears to reduce the ability of neurons to encode rapidly varying ones [54, 55].

3.4.4 Plasticity

There is also evidence that the addition of noise improves certain aspects of learning in artificial neural networks. It improves the network's ability to generalise, makes it more resistant to mistakes and speeds up the learning process. What is more, these results appear to be generalisable over different training schemes and could be applied on a variety of real world problems [56].

3.4.5 Computation

The computational capabilities of spiking neural networks have also been the subject of study for several years. Much is now known about the dynamics of information and the computational power of spiking neural populations [57–59]. Networks of spiking neurons can be shown to be more powerful, with respect to computation, than their notional predecessors, binary and analogue neural networks [59]. Therefore, it follows naturally to ask what the effect of noise would be on the computational capabilities of spiking neural networks. Research has shown that under specific circumstances noise can improve the computational power of spiking neurons [60, 61].

3.4.6 Information transmission

It quickly becomes obvious that noise in a spiking neural system improves information transmission [10, 11, 27, 28, 53]. However, concrete evidence is needed to prove that improving information transmission is equivalent to improving information processing. In other words, does the fact that more information is flowing through the neural system make it a more powerful computational agent?

In order to answer this question, a framework is needed that can be used to study the dynamics of information in a neural system. A good candidate for this task is Information Theory (IT), not only because it already has a variety of tools with which to study neural systems and their information transmission and processing properties but because it also allows us to draw analogies between neural networks and other information processing systems. Further discussion of this framework is given in Chapter 4.

The next logical step after determining whether noise has any beneficial effects on information processing, is to determine whether we can harness these effects in order to design neural systems with improved information processing capabilities. Some attempts have been made to optimise specific phenomena with a certain degree of success [8, 62], but a lot remains unanswered.

On the one hand, understanding the interplay of stochasticity and information in artificial neural systems would shed light on how noise is affecting the performance of biological neural networks. It becomes more and more evident that noise is not necessarily a hindrance to information processing and that it may very well be a vital part of the cognitive processes of the brain. This research can show in what ways this is achieved. On the other hand, analysing the phenomena due to stochasticity in artificial neural systems can lead to the development of optimisation frameworks that will allow us to design and implement more powerful computational systems.

3.5 Summary

The sources of stochasticity in biological neural systems were presented along with ways to introduce them in computational neural models. A choice was made in terms of noise methodology and justification was given. A study of the effect of noise was made and an exploration

of the phenomena observed along with ways to study and exploit them further.

Chapter 4
Information theory

Neural networks, both biological and artificial, and their underlying mechanisms are very important to us because of their impressive computational capabilities. Quantifying these capabilities, and any changes in them, is crucial. In order to achieve this goal we need an appropriate framework with tools that provide an accurate depiction of information dynamics inside a neural network. These tools need to also link intuitively these results to those of other information processing systems.

A framework that fits this description and one that has been used extensively to study the information processing capabilities of neural networks, both biological and artificial, is information theory (IT). However, information theory is not an uncontested candidate for this task. Even though it is more than appropriate for the purposes of rigorously analysing mathematical systems, it is very important to show that it is an appropriate set of tools for analysing biological or biologically inspired and accurate information processing systems.

We need to determine exactly how meaningful are the answers that information theory as a framework provides us with. This work attempts to contribute, using information theory, to the understanding of how neural networks filter information from their stimulus environment. It also attempts to provide the limits of a neural code employed by a neural population and what those limits signify. Information can determine how much information a single neuron, and various populations of neurons, actually transmit. As any approach it has its limitations but it is shown that there are hints at an optimal encoding and information transmission strategy in all the seemingly chaotic activity of a neural population. More importantly, there is evidence that such a strategy exists and it can be exploited in order to design better artificial neural networks. These are the tasks with which information theory, and any other candidate framework, is faced when applied to the study of the information processing capabilities of neural networks. Some of these questions have been investigated thoroughly, both in this work and elsewhere. Some of them have been answered whereas some of them remain, at least to some degree, unanswered [10–13, 45, 52, 54, 63–73].

4.1 Why information theory

Intuitively, it is known that neurons and their responses convey information. At least in principle, when we observe the neural response we gain information about the nature of the input that produced it. However, precise measurements of these intuitive notions need to be made. This line of research leads to the precise characterisation of the neural systems performance in terms of information transmission. It can give a quantitative measure of neural performance in agreement with intuitive notions and also places the information measurements that might be made on an absolute scale. This in turn allows meaningful conclusions to be drawn about information dynamics in a neural system in itself or in comparison to other computational systems.

4.1.1 Entropy and available information

Before observing the neural response, it is known that stimuli presented to the neural system both in the natural world but also under experimental conditions, are not equally likely. They have limits and probabilities, in short, statistics. These limitations can be pictured delineating a finite size in the stimulus space, for example an area or a volume. Observing the neural response, and assuming that the neural system has a relatively consistent encoding scheme, narrows down this area or volume in the stimulus space. This reduction in size of the range of possible stimuli, measured on a logarithmic scale, is equivalent to the information provided by the neural response, measured in bits.

In order to begin studying and understanding information dynamics in neural systems, first we must try and characterise any neural system as a standard communication or information transmission channel. This channel is presented with input X, where X can be any signal as a function of time, and encodes it into output Y, where Y is a set of spike timings. In both cases of natural or experimental conditions, an input signal is chosen from a probability distribution $P[X]$. Returning to the picture of all the possible stimuli as an area or a volume, which is also a depiction of the probability distribution $P[X]$, we can also start to consider the amount of available information. If this range of values is too small, that is only one value is possible as an input, then the message that travels through our communication channel is always the same and therefore no information is transmitted.

This gives us a notional starting point for understanding how to quantify available information. The range of the possible values that the input can take is clearly connected to the amount of

information that can be transmitted. The same is true for the output, if output Y is always the same then there is no information transmission. Consequently, in order to quantify the availability of information in a signal we need to measure the variability of the signal. The most appropriate measure for this task is entropy and has been shown to be the only measure that fulfils certain necessary requirements for the task at hand.

4.1.1.1 Entropy of discrete and continuous signals

Entropy is the logarithm of the number of possible states the system can be in. This means that if the input signal X is a discrete variable with values $x_1, x_2, ..., x_K$ and a uniform distribution, its entropy $S(P[X])$ is proportional to $\log K$. If the signal is discrete but its K possible values have unequal probabilities then the entropy is formally defined as

$$S = -k \sum_{i=1}^{K} p_i \log p_i, \tag{4.1}$$

where p_i is the probability of observing the i^{th} possible value and k is a constant [74]. This expression can be naturally generalised for the case of a continuously valued signal so that instead of dealing with a set of discrete probabilities, we can now work with a probability distribution function $P(x)$. In the case of a continuous variable, entropy is defined as

$$S = -k \int dx P(x) \log P(x). \tag{4.2}$$

Conventionally, the logarithm's base is chosen to be two in order to obtain the amount of available information in bits. In the case of a discrete variable and by choosing an appropriate base for the algorithm that eliminates the constant k, entropy can then be defined as

$$S = -\sum_{i=1}^{K} p_i \log_2 p_i. \tag{4.3}$$

On the other hand, in the case of continuous variables, measuring their entropy can be problematic if we consider the fact that a continuous variable has an infinite number of possible states. However, since all measurements rely on the degree of precision with which they are made, which is always finite, the entropy of a continuous variable can be calculated if the variable is

discretised.

4.1.1.2 Entropy of a spike train

Entropy is a very useful tool in our attempts to understand the neural code since it provides us with limits to the information that the neural system deals with. More precisely, the entropy of the input signal is the upper limit on the amount of information that can be made available to the system. This raises the issue of careful experiment design and the need to provide neural systems with adequately information rich signals. The other limit set by entropy is the amount of information the neural response can provide about the system's input, even if that is a theoretical approximation.

The first application of information theory to the study of neural systems occurred very soon after the former's development and provided a very useful approach to studying the neural response [75]. Assuming that the neural response under observation is recorded with a specific and finite temporal resolution which allows for a spike to either be or not be in any single time bin, the neural response can then be thought of as a binary sequence in which 1 denotes the occurrence of a spike and 0 the non-occurrence. Obviously, the two numbers do not occur with the same probability. In fact, there is a limit to the kind of binary strings that can be observed in any sequence which is imposed by the maximum firing rate that any neuron can achieve and maintain.

Measuring the entropy of spike trains provides a tangible measure of how much information is in a particular signal. It can also give an information rate of bits per second or even the information conveyed by a single spike [9]. What this means is that entropy is an extremely useful tool in assessing different encoding schemes and their capabilities.

If the input signal with which a neural system is presented is varying slowly with time and the resulting spike trains are divided into time windows that contain many spikes, then all of the spikes in any specific time window will tell something useful about the characteristics of the stimulus that did not change, approximately, during that time window. This approach, can elucidate the kind of code that is being used, timing or rate, because it can be used to measure which of the two characteristics of the neural response, spike timings or overall firing rate, conveys more information about the stimulus during that specific time window. The distinction between the two becomes less obvious when the time window is much smaller so that the

average number of spikes in time windows is much smaller than 1. If the stimulus with which the neural system is presented varies on a time scale comparable to the size of the time intervals in the neural response then any time window will contain few spikes making it more likely that a timing code is used. All of the above point towards the conclusion that the coding scheme of a neural system is not something set in stone and depends on the nature of the stimulus. What is more important though is that this shifts the focus from the question of rate coding versus temporal coding towards the much more relevant question of what would the best encoding scheme be for this input signal?

Another way to look at the entropy of a spike train is as the physical maximum amount of information that the specific spike train can convey about any kind of signal. Under an ideal coding scheme each spike train would represent a single stimulus and the entropy would measure the actual amount of information contained in the spike train about the stimulus. The more we diverge from this ideal code, the less accurate entropy is as a measure of information gain.

4.1.2 Mutual information

Entropy is a very useful tool in the study of neural systems, their activity and the flow of information within them, but it can only go so far. By definition, entropy is a measure of the maximum possible information that can be contained within a signal. However, entropy cannot tell us how much of that information is actually there and what part of it is information about the input signal that has been conveyed by the neural system and is encoded by the output. In order to characterise this kind of information, that is the amount of common information between the two signals, stimulus and neural response, mutual information is used [9].

In this case too, the same assumptions are made as in the case of entropy. This means that input signal X is taken from a known probability distribution $P[X]$ and that there is a reduction in the variability of the range of possible input signals once the output signal Y has been observed. Mutual information or the amount of information that is common between input and output can now be formally defined [9].

Where the entropy of $P[X]$ measured the range of possible input signals after observing output Y, the reduced variability of X is now described by the entropy of the conditional probability distribution $P[X|Y]$. This probability measures the relative probability of various input signals X given that we have observed a specific value of Y. Assuming that only a small subset of

the possible signals X could cause any one output signal Y, then the entropy of the above conditional probability distribution is called conditional entropy and is defined as

$$S[X|Y] = -\int [dX] P[X|Y] \log_2 P[X|Y]. \tag{4.4}$$

Intuitively, the conditional entropy is a smaller number than the total entropy $S[X]$ since it measures the variability of a smaller set of signals. This reduction or difference between entropies is the amount of information gained by observing the output Y. Averaging over all the values of Y gives us the mean information gained

$$MI = \int [dX] P[Y](S[X] - S[X|Y]). \tag{4.5}$$

This measure of average information gained by observing the output signal Y is also called mutual information. Mutual information (MI) is a symmetric quantity which means that we can think of events in the neural response as giving us information about what is happening in the signal the neural system is observing or we can think of changes in the stimulus as predictors of the neural response. In either case, the amount of information is identical [9].

Another useful way to think about mutual information is to consider X and Y momentarily as independent variables chosen from probability distributions $P[X]$ and $P[Y]$ respectively. In this case, the entropy $S[X, Y]$ of this system is the sum of the two entropies $S[X]$ and $S[Y]$, each associated with the respective variable. However, these two variables are correlated so the entropy of the whole system is actually smaller than the sum of their entropies. The difference between the entropy of the system and sum of the two entropies of the variables gives us another useful definition of mutual information

$$MI = S[X] + S[Y] - S[X, Y]. \tag{4.6}$$

Yet another way to view this quantity, and one that is very useful for the purposes and experimental setup of at least a part of this body of research, is to consider the neural system as an information transmission channel in which there is additive noise. This system can be roughly described as $y = a(x + n)$ where x and y are the, by now familiar, input and output signals, a is the factor by which y is proportional to x and n is a noise factor added to the signal which

for the purpose of simplicity can be thought of as having a Gaussian distribution [9].

Another, very important reason for choosing a Gaussian distribution is that this kind of distribution is very common in nature, especially when the quantity under observation is the sum behaviour of a large number of independent random processes such as ion channel stochasticity. Mutual information is the difference between the sum of the entropies of the input and the output and the entropy of the system as a whole (see equation 4.6). We have described the neural system as an information transmission channel and we know the input x and the noise n and that they are variables independent of each other. We can now describe the system entropy $S(x, y)$ as the sum of the entropies of the input signal and the noise

$$S(x, y) = S(x) + S(n). \tag{4.7}$$

This leads to a very useful alternative definition of mutual information. By substituting, we can see that mutual information is the entropy of the output signal minus the entropy of the additive noise

$$MI = S(y) - S(n). \tag{4.8}$$

This means that if there were no noise, every input signal would correspond to a single output signal and that our information gain after observation of the output would be the entropy of the output. By subtracting the entropy of noise when noise is present in the system we obtain a much more accurate estimate of the information transferred since in the presence of noise the entropy of the output is an overestimate of information transmitted. Notionally, this verifies the fact that output entropy puts a physical upper bound to transmitted information. In the particular case of a neuron, this means that the upper limit of what a neuron can transmit about the input it receives is the entropy of its resulting spike train [9].

Information transmission cannot be measured in the literal sense [9]. Any attempt at calculating it is bound to produce an estimate which we can try to make as accurate and as controlled as possible. In order to make a controlled estimate that could provide us with a lower bound for the information transmission rate, we need to know and understand at least some of the intricacies of the system under study. In this case, making a meaningful estimate of information transmission requires some understanding of the neural code. This also means that information

theoretic analysis and the understanding of the neural code are interlinked and that advances in the study of one can lead to greater understanding of the other.

4.1.2.1 Information transmission with discrete and continuous signals

In some cases, mostly under experimental conditions, the stimulus is a discrete variable by its nature or is discretised by the experimenter in order to simplify the analysis. However, this is a simplification and it can introduce a greater degree of ambivalence as to how accurate is an information theoretic analysis based on this kind of experimental setup. Neurons can transmit a great amount of information and in order to study the true information content of the neural response one should choose stimuli similar to those in the natural world and ones that change more realistically with time [9].

When presented with temporally rich signals, biological neurons will attempt to encode as much information as possible into their response instead of filtering out potentially biologically irrelevant information. This means that natural world signals or signals that closely approximate naturally occurring ones push the neuron close to its limits of information transmission [9]. All of the above are the justification for using continuous stimuli for the purposes of information theoretic analysis in every experiment performed for this body of work, unless otherwise stated.

4.2 Information maximisation

Information theory is a very powerful framework and one that provides us with tools that can place neural systems on an absolute scale of information processing capabilities. This makes information theoretic analysis the most appropriate approach for studying the effect of noise on the information dynamics of neural systems. Information theory has been used extensively in the context of stochastic neural systems thus laying a solid foundation for answering the question of what role noise plays in the nervous system.

4.2.1 Positive effects of noise

Here we will revisit phenomena that were presented previously but this time with a focus on their information theoretic aspect. The most important phenomenon when it comes to studying information transmission in neural systems under the influence of noise is stochastic resonance

and its extension into the frequency domain, coherence resonance. Information theory gives us a greater understanding of this seemingly counter-intuitive mechanism.

In the case of the simplest neural system available, a single neuron, stochastic and coherence resonance are well studied and documented [10–13, 52, 54, 63, 64]. From an information theoretic point of view, stochastic resonance can be easily explained. As noise is added to the input signal, the entropy of the signal increases. This is intuitive, more variability is added to the signal, therefore entropy, and consequently the upper bound of available information, increases. The same is true for the output signal. Consequently, the sum of the two signal entropies increases as well. The entropy of the system as a whole increases too. However, initially it does not increase as quickly as the sum of the signal entropies. The difference between these two quantities, that is mutual information, initially increases, reaches an optimum and after adding further noise starts decreasing. So where available information in both signals and the system increases with the addition of noise, the amount of information added by noise that is useful for the transmission of information included in the signal increases only until a specific amplitude of added noise. In short, noise adds available information to the system which the neuron can use to improve the transmission of information about the signal. Another very useful way to visualise the effect of noise on the amount of available information and on information transmission is based on equation 4.8.

Using this we can understand the effect of noise on the neuron and the neural response more directly. The amount of available information in the spike train increases as we add noise and so does the entropy of the noise since an increase in amplitude signifies an increase in variability. For lower noise amplitudes, available information in the spike train increases faster than the entropy of noise, an optimum is reached and then noise starts having a destructive effect. This suggests that until the optimum noise level, the neuron is incorporating information provided by the noise into the signal in order to improve information transmission of the signal.

Similar phenomena can be observed in populations of neurons, arrays or more complex networks, and in a variety of circumstances [27–29]. In some cases it is suggested that there is no need to calculate a noise optimum in order to improve information transmission in a population of neurons [76]. It quickly becomes obvious that noise can play a very positive role in a neural system, whether that is a single neuron or a complex population of neurons, in terms of information transmission. However, some questions arise as a result of this approach. Noise can improve weak signal detection and it can improve information transmission about the input

signal. But perhaps there is a good reason for weak signals to not be detected in a neural system. Maybe it is a good strategy to not try and encode and transmit everything about the signal that is presented. To answer these questions and remove any kind of ambiguity from the effects of noise on neural activity we need to elaborate on the results obtained with information theory.

4.3 Stochastic phenomena in a spiking neural network

In order to make sure that the general theoretic background is valid for the neuron model used in this work and also to create an experimental foundation for elaborating on the results obtained using information theory, some initial experiments were carried out concerning already well known quantities of neural system information dynamics. The standard experimental procedure, unless otherwise stated, involved experimentation with one stochastic spiking neuron and, eventually, a small population of stochastic spiking neurons and the use of information theoretic tools starting from the simplest one, entropy, working up to more complex ones. This should provide a clear delineation of the limitations of an information theoretic approach, possible strategies to overcome them as well as additional proof of the usefulness of information theory as a framework for the study of information dynamics in larger and more complex neural systems.

4.3.1 Entropy

The first step in this approach is to measure the amount of available information in the input and output signals and the system entropy under the influence of additive Gaussian noise of increasing amplitude. This provides us with the available information in the input signal, the upper limit of possible information content in the spike train as a response to the input signal and the amount of available information in the system as a whole. This methodology, however, is slightly problematic. In a practical, computational context, the entropy of an analogue value is hard to compute and depending on the degree of discretisation, its estimate can be extremely inaccurate. One way around this problem is to know the probability distribution from which the signal is picked and thus calculate the entropy. This approach is inadequate as well, since it is also an estimate and depending on the length of the signal, it can be inaccurate. Another way to overcome this obstacle is to use digital input signals or to discretise the analogue signal with an arbitrary resolution. This does make calculating the entropy easier but it clearly makes for even

more inaccurate estimates since part of the signal is thrown away. In any case, providing a neural system with digital input is underestimating the system's information processing capabilities since it has been shown that neurons transfer more information when presented with continuous signals that have rich temporal characteristics [9]. For these reasons, but also for computational simplicity, the neural systems under study in this series of experiments, whether a single neuron or an entire population of neurons, were presented with continuous stimuli. Calculating the entropy of continuous variables was avoided as much as possible since it eliminates a degree of uncertainty which would provide increasingly inaccurate estimates of information theoretic measures based on entropy.

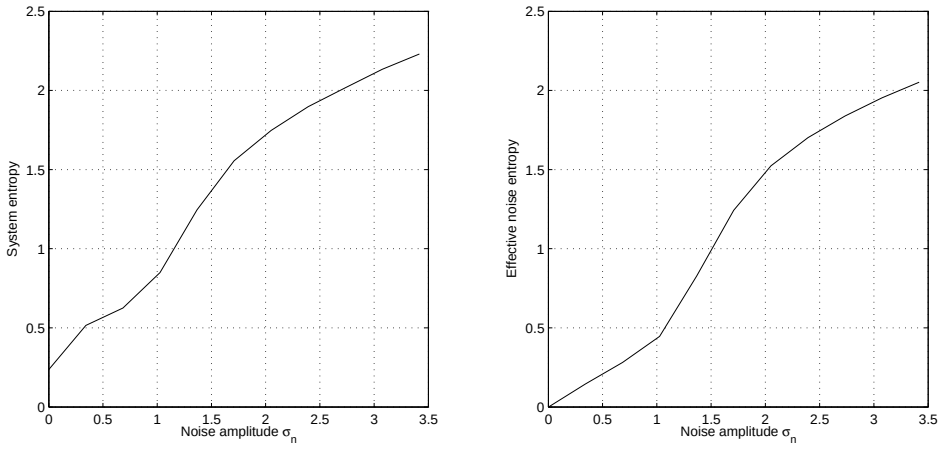

Figure 4.1: *Entropy in a population of spiking neurons. On the left, system entropy of a population of 100 Izhikevich neurons under the influence of increasing noise amplitude. On the right, effective noise entropy for the same population.*

4.3.2 Mutual information

The need to circumvent the calculation of the entropy of a continuous variable becomes more apparent when one attempts to measure information transfer through a neural system. An inaccurate estimate of a continuous variable used to calculate the mutual information between said variable and another one, would provide an inaccurate estimate of the information transmission. In order to overcome this problem, equation 4.8 was used. This definition of mutual information ignores the nature of the input signal and is based on the entropy of the spike train which can be very accurate since the neural response is a binary signal. It is also based on the entropy

of the effective noise which can be estimated to any desired degree of accuracy. Measuring the mutual information between the input and output signals of a neural system then becomes a simple task of data collection and statistical analysis.

The system is presented with the same input for a large number of times, the neural response is recorded every time and the degree of variability between all of the responses is measured. This is the entropy of the effective noise. The difference between this entropy and the entropy of the neural response is the amount of information transmitted. This approach provides an estimate of mutual information regardless of what the input signal and its entropy are, whose accuracy depends solely on the number of times the input is presented to the system. Accurate and useful as that may be, it will become evident that in the context of information transmission optimisation this approach too is untenable.

4.3.3 Integration

Entropy and mutual information form the groundwork for further analysis of the information dynamics of a neural system. They are numerical representations of physical quantities, namely the maximum possible amount of available information in a signal and the transfer of information through a system respectively. They offer a useful insight into the workings of a neural system, particularly if the system under study is a single neuron. Since one of the primary functions of a neuron is to transmit information, entropy and mutual information can give us an adequate picture of just how good at this task a single neuron can be. However, this is not exactly true for the case of an entire network. The functions of a neural population include but are not exhausted by transmission of information. Entropy and mutual information provide some useful insight but do not paint the full picture of information dynamics inside an ensemble of neurons. The availability of information in a neural population does not guarantee that this information is being used in some way and transfer of that information does not necessarily have a positive effect on the computational potential of the neural system.

This notion creates the need for more sophisticated measures of information dynamics. In the case of a neural population, employing mutual information is of limited consequence since at best an estimate of the information flow between the population and its surroundings is obtained. This of course can be extremely useful depending on the experimental focus. However, if one wants to study the internal mechanisms of information processing inside the neural population a measure is needed that can elucidate, at least at first, information flow between the

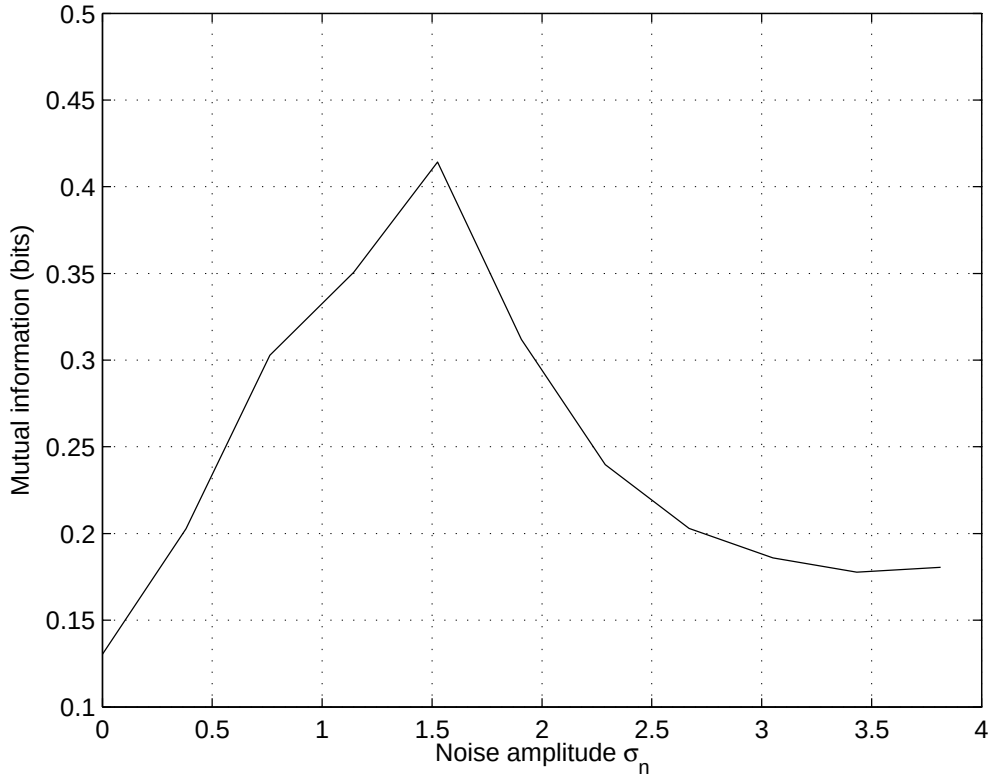

Figure 4.2: *Mutual information in a population of spiking neurons. The characteristic signature of stochastic resonance in the mutual information of a population of 100 Izhikevich neurons. Mutual information is calculated using the entropies shown in Figure 4.1 and equation 4.8.*

subunits of the system.

By extending the concept of mutual information one can use such a measure for this purpose. Integration is a measure that quantifies the degree of dependence between the subunits of a system such as a neural population [77–80]. It can be defined as the sum of the entropies of all of the system's components, in this case all of the neurons, minus the entropy of the system as a whole

$$I = \sum_{i=1}^{n} S(x_i) - S(X), \tag{4.9}$$

where X denotes the system as a whole, x_i represents each individual neuron and n is the number of components or, in this case, neurons in the system (see Figure 4.3).

However, there is a formulation that explains more easily the physical notion that underlies this quantity. It can be equated to the sum of mutual information values for every possible pair of parts resulting from a bipartition of the system [78]. Put more simply, it is a measure of how well each possible sub-population of neurons communicates with the rest of the population. This is a fairly tangible quantity to calculate in a computational and experimental context even for networks comprising several tens, or possibly hundreds, of neurons. Integration is a good first step in assessing the flow of information between different parts and components of a neural system but it too has its limitations.

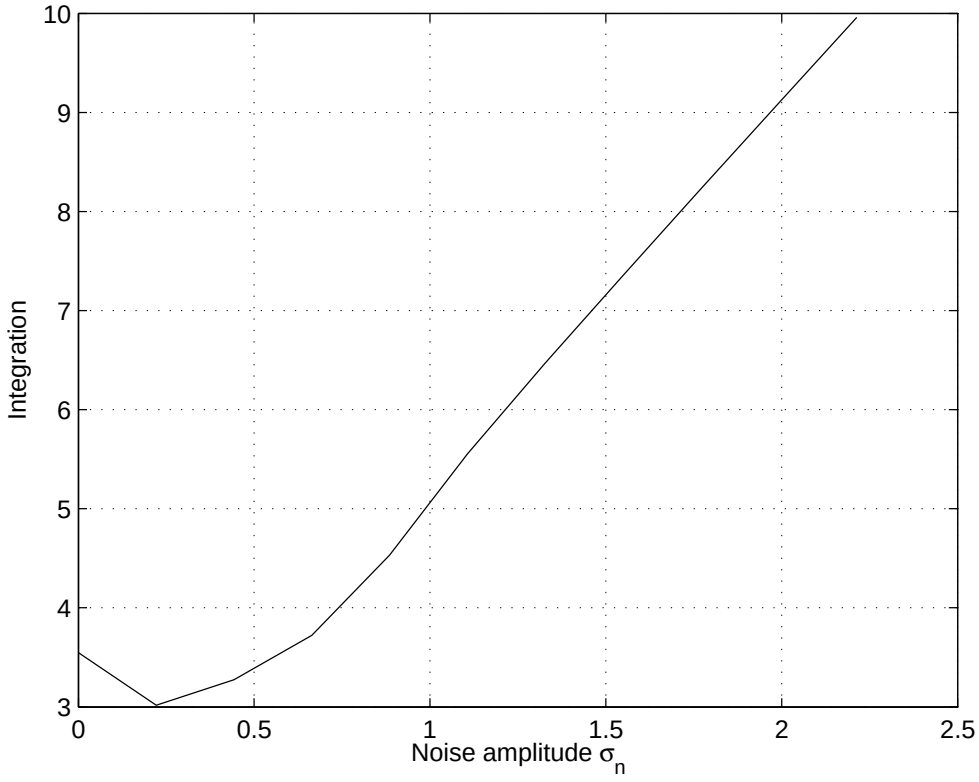

Figure 4.3: *Integration for a population of spiking neurons. Integration for a population of 100 Izhikevich neurons under the influence of noise of increasing amplitude is calculated using equation 4.9. This result signifies the functional integration of the network and its components. It shows the increasing amount of shared information among the population's components as noise amplitude increases.*

4.3.4 Neural complexity

The most important shortcoming of Integration becomes obvious when one considers its name. Integration measures the functional integration of components and sub-populations in a neural population. This means that the more information the components share, the higher the value of integration will be. However, if parts of the system shared more and more information they would become more and more coupled and finally indistinguishable from each other in terms of activity. Intuitively, this can in no way make the neural population a more powerful computational system.

Instead, we need a measure that embodies both functional integration and functional segregation at the same time. Neural complexity is exactly such a measure. The complexity of any system X is defined as the difference between the average integration values for subsystems of size k, where k can be anywhere between 1 and the total number of neurons in the population, and their expected values resulting from a linear increase in subset size [78]. This notion is formulated as

$$C_N(X) = \sum_{k=1}^{n} [(k/n)I(X) - \langle I(X_j^k)\rangle], \tag{4.10}$$

where X_j^k is the j^{th} subset of system X with k components. This means that neural complexity increases as integration increases while at the same time the average integration for small subsystems in the population is lower than would be expected from a linear increase in subsystem size [78]. Neural complexity can also be expressed in terms of entropy

$$C_N(X) = \sum_{k=1}^{n} [\langle S(X_j^k)\rangle - (k/n)S(X)] \tag{4.11}$$

or mutual information

$$C_N(X) = \sum_{k=1}^{n/2} \langle MI(X_j^k; X - X_j^k)\rangle. \tag{4.12}$$

It follows that complexity can be expressed as the average mutual information between bipartitions of X, summed over all bipartition sizes. Notionally this translates to an increase in

complexity when there is an average increase in the mutual information between any subsystem and its complement in the neural population (see Figure 4.4). Complexity is a very powerful tool for studying the effect of noise on information dynamics in a neural population. However, because its calculation requires to average over a large number of subsystems, the number of which quickly explodes as the number of neurons in the population increases, it very easily becomes impossible to calculate it directly. Instead, approximations must be made and even those can be computationally demanding [78].

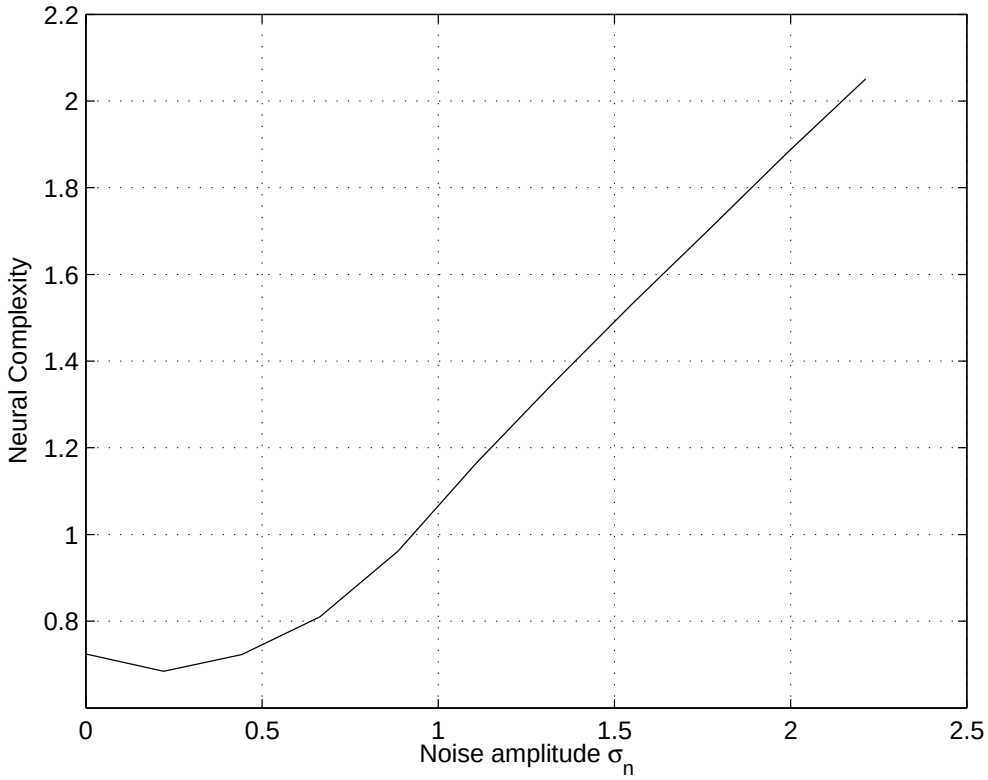

Figure 4.4: *Neural complexity of a population of spiking neurons. The neural complexity of a population of 100 Izhikevich neurons under the influence of noise of increasing amplitude is calculated using equation 4.11. Neural complexity quantifies the balance between functional integration and segregation among the components of neural system.*

4.4 Optimising the positive effects of noise

As we have seen above, information theoretic analysis offers useful insight into the underlying mechanisms of information dynamics and provides us with the foundations needed for the development of an optimisation framework based on the role of noise in a neural system. However, before embarking on the development of optimisation algorithms based on the results obtained using information theoretic measures one must evaluate these results with respect to their suitability as optimisation criteria.

4.4.1 Information theoretic measures as optimisation criteria

Entropy provides us with a quantification of the available information in a signal or a system. It is the upper bound on the amount of information that a signal or system could possibly convey. At first sight, it could very easily form the basis for the development of an optimisation algorithm. However, adding increasing noise to a neural system increases the entropy (see Figure 4.1) without any visible optimum. Also, notionally this approach would be problematic since an increased amount of available information does not signify an improvement in information processing. More simply put, the fact that there could be more information in the system cannot be equated with having more useful information in the system.

On the other hand, mutual information is much more useful as an optimisation criterion since it is a measure of transmitted information, a concept which is intimately connected to the function of neural systems. In fact, mutual information has been used extensively to study and optimise information transmission and, more generally, information maximisation is considered to be a valid optimisation criterion [8, 11, 27–29, 62, 81–83]. It also makes stochastic resonance obvious, a phenomenon which occurs under the influence of noise (see Figure 4.2) and forms an excellent starting point for improving information transmission.

Integration on the other hand, as a measure of deviation from independence [78] provides us with a useful measure of the information communicated between the components of the system, but cannot be used as an optimisation criterion of a stochastic neural system. This is because an indefinite increase in integration signifies the increasing dependence of subsystems and components on one another and consequently a reduction in functionality. It also becomes obvious from experimental results that integration on its own could not be used as an optimisation criterion for stochastic neural systems.

Neural complexity, the incorporation of integration along with functional segregation, would be a much more appropriate quantity to use as the driving force in an optimisation algorithm. It provides us with a measure of information flow balanced between component dependence and independence [78]. It gives us valuable insight into the information dynamics of a neural system and it also demonstrates clearly what the effect of noise is on a higher level of neural organisation.

4.4.2 Limitations

It becomes quickly evident that even though all of the information theoretic measures presented are very useful tools in the study of information dynamics in a stochastic spiking neural system, not all of them can be used effectively for optimisation purposes. Entropy and integration are unbound measures, in the sense that they keep increasing with increasing noise amplitude in the system. Consequently, even if they are, initially, measuring a positive effect of noise on the system, it would quickly become masked by the destructive effects of noise. Neural complexity, on the other hand, which at least notionally should be extremely useful as a measure of information processing capabilities, is a very costly quantity to calculate from a computational point of view. It quickly becomes intractable with even a small increase in the number of neurons in the system [78]. This does not necessarily make it impossible to use but makes it a highly unlikely candidate for optimisation unless an appropriate approximation can be made. This leaves mutual information which has been proven to be a valid optimisation criterion for a stochastic neural system [8].

4.4.3 Online optimisation

All of the above raise important questions. What is the optimisation framework based on which we judge the suitability of the aforementioned information theoretic measures? Because of their statistical nature these measures are used mainly for the purposes of analysis. Optimisation is usually a process that requires rapid responses to changes in the neural system's surroundings. Can we really talk about optimising a neural system's information transmission in response to a stimulus when the stimulus has to be presented hundreds if not thousands of times to the system? Is such an optimisation meaningful when we know that neural systems have an entirely different response and very likely encode stimuli in their responses differently? Perhaps it is appropriate to consider an online information theoretic optimisation approach for stochastic

neural systems. Perhaps it is the most appropriate approach. However, it is clear that information theory is not designed to be an online optimisation framework. It is an analytical tool-set and a computationally complex one at that, which begs the question of how can we use it for such a purpose? How can we transform a powerful analytical framework into an optimisation framework for stochastic neural systems? These questions are answered in the following chapter.

4.5 Summary

In this chapter, Information Theory was introduced, analysed and justified as an analysis and optimisation framework. Distinct and increasingly detailed and complex measures were explained. Entropy, mutual information, integration and neural complexity were detailed in turn and their advantages and shortcomings were explained. They were all judged on their ability to be used in a noise optimisation framework and mutual information was deemed to be, justifiably so, the most appropriate measure.

Chapter 5
Optimisation

As mentioned in the previous section, mutual information and information theory in general can be a very powerful tool in the study of neural systems but more particularly it can offer valuable insight into the effects of noise on information dynamics.

5.1 Information transmission systems

Mutual information quantifies the amount of information that is common between two signals. In the case of a neural system, mutual information gives us a natural quantity on an absolute scale about how much of the stimulus presented to the system is represented in the system's response. This means that with mutual information we can obtain a measure of how good an information transmission system is at what it does, regardless of whether that system is a single neuron or an intricately interconnected neural population.

Therefore, mutual information and information theory in general provides us with a solid foundation for developing an optimisation framework of stochastic neural systems. It gives us the necessary notional and analytical background for elucidating the underlying mechanisms of stochastic neural information dynamics and also serves as a guideline for conceptualising an optimisation algorithm.

5.2 Computational cost

Unfortunately, as with most of the complex quantities in information theory, mutual information requires a large amount of data in order to be calculated to an adequate degree of accuracy. An amount of data that makes the notion of online noise adaptation based on mutual information seem impossible [8]. The same stimulus would have to be presented to the neural system a few hundred times, with the only variability in the system being due to additive noise, before any attempt at estimating mutual information between stimulus and neural response can be made.

Since such a large amount of data is required, computational costs rise accordingly. Presenting the same stimulus to a single spiking neuron several hundred times and then performing statistical analysis on the resulting neural responses may be a trivial task that only takes a few minutes on a personal computer, but the same cannot be said about a network comprising of a few hundred neurons. In that case, this method for the calculation of mutual information becomes a more difficult, if not intractable, problem which makes the extension of such an approach to more complex neural systems seem like a dead end.

5.3 Online optimisation

Regardless of the computational cost, this statistical approach faces a more serious obstacle which ultimately makes it inappropriate as an optimisation methodology in itself. This method cannot be applied online. Presenting the same stimulus to the neural system a few hundred times guarantees that this methodology bears no resemblance to any online adaptation approach. Additionally, in any real world situation, possibly in most simulations too, the stimulus changes quickly enough for any optimisation of the amplitude of additive noise inside the neural system to become obsolete very quickly. Consequently, such an approach would be inappropriate and ineffective for any real world and online situation. It is also doubtful whether it could be a biologically plausible one.

5.4 Mutual information as an optimisation criterion

The question then becomes of finding an approximation or an equally valid candidate for optimisation as mutual information and one that will also be notionally, and hopefully numerically, connected to it. Intuitively, such an approach may suffer in terms of accuracy. However, it will provide a useful and, more importantly, extensible optimisation framework.

5.4.1 Equivalent quantities

Any such measure should, at least notionally, be equivalent to mutual information. If it can also give us a natural and absolute quantification of information transmission through a neural system, then it is a perfect candidate for replacing mutual information, at least in the case of an online optimisation paradigm.

Mutual information is conceptually and numerically connected to the mean square error between the stimulus presented to the neural system and an estimate of the input given the neural system's spike response [84–86] (see Figure 5.1). Mutual information between input and output has also been shown to be an appropriate criterion for optimisation in the same way that the mean-square error between stimulus and stimulus estimate is [86]. This connection has been shown to be true for information transmission channels such as a neuron and has been generalised [84]. Therefore, it serves our purpose of finding some degree of equivalence between mutual information and a simpler quantity.

By developing a stimulus estimator that will generate an estimate of the input using only the neural response to that stimulus, the first step towards developing an online noise optimisation framework can be taken.

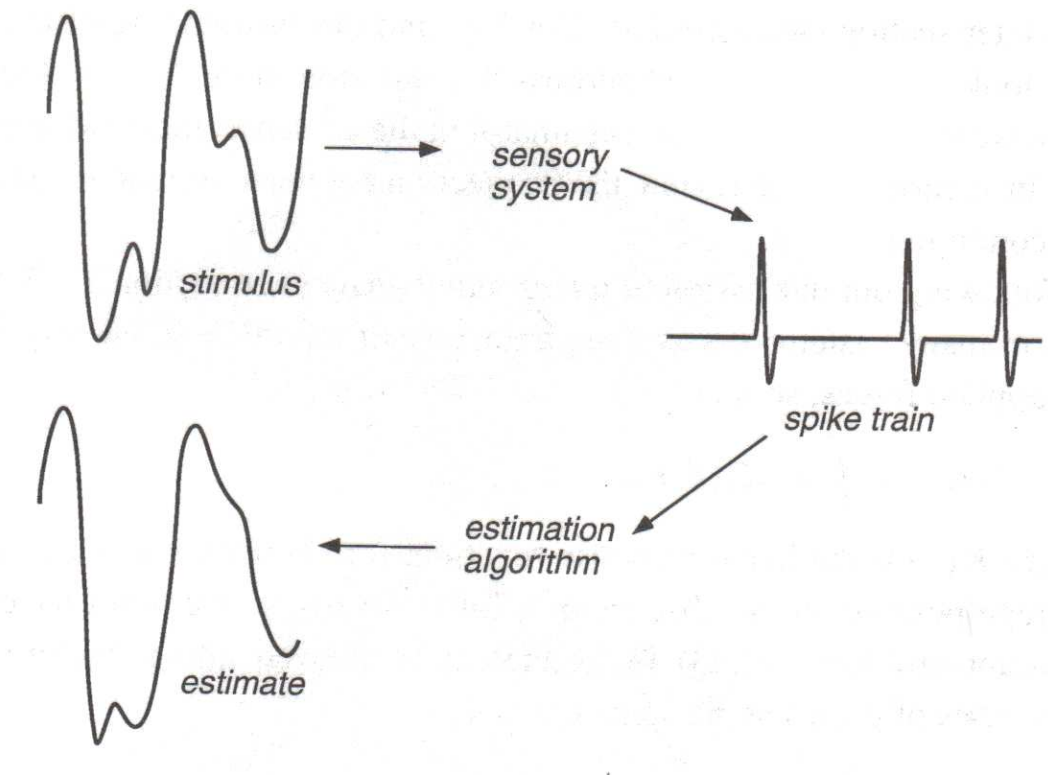

Figure 5.1: *Stimulus estimation and reconstruction. A diagrammatic view of how stimulus reconstruction works. Figure from [9].*

5.4.2 Stimulus estimation

Obviously, to take that first step, an adequate estimator is required. In the case of stimulus estimation using spike trains, the general consensus is the use of linear reconstruction filters [9]. These filters are also referred to as decoding filters and are more commonly used in order to visualise and quantify the precision of information transmission and to characterise the encoding capabilities of neural systems. Assuming that the important characteristics of the spike train are in the timings of the spikes, the linear reconstruction filter takes the form

$$s_{est}(t) = \sum_{i=1}^{N} K_1(t - t_i), \tag{5.1}$$

where s_{est} is the input estimate and $K_1(t - t_i)$ is the linear response to a spike in the neural activity. This methodology is a perfect candidate for designing an online noise optimisation algorithm for a number of reasons. The most important reason and a characteristic without which the prospects of developing an online optimisation framework are rather poor, is the ability to provide a stimulus estimate, and consequently the mean square error between stimulus and estimate, with a single set of data.

Presenting the neuron with the stimulus just once, assuming the presentation is long enough so as to obtain enough spikes in the neural response, provides more than adequate data in order for the linear reconstruction filter to estimate the stimulus. This cuts down on computational costs dramatically, and moves the use of information transmission capabilities as a noise optimisation criterion from the realm of the unlikely to that of the not only possible but also very effective.

Consequently, linear stimulus reconstruction is that very first step that needs to be taken in order to develop an online noise adaptation scheme. Not only because it works, but also because it gives us insight into the encoding dynamics of the neural system.

5.5 Signal reconstruction

Starting from the simplest neural system possible, a single spiking neuron, stimulus estimation with the use of linear reconstruction filters was used. This was done first and foremost to judge its ability to reconstruct the stimulus that was presented to the neuron and then to determine whether the input estimate it would provide is indeed appropriate for use as a component in an

information transmission optimisation algorithm.

As mentioned above, this methodology is primarily used by other researchers in order to decode neural activity in a variety of experimental settings [9, 87–93]. In this particular body of work, the ability of a linear filter to reconstruct the stimulus given the neural response is used as an intermediate step in the process of optimising information transmission under the influence of noise.

This is achieved with a remarkably small amount of data. In order to obtain an accurate estimate of the stimulus, and consequently an accurate estimate of information transmitted about the input, instead of needing several runs of the spiking neuron while presented with the same stimulus, only a single run is needed. The only limiting factor in this case being that a certain number of spikes are needed to construct an accurate linear filter before it can be used to provide accurate estimates of the stimulus based on the resulting spike train.

For the purposes of stimulus reconstruction from spike trains in the case of a single spiking neuron, a Wiener-Kolmogorov (WK) filter was chosen as it has been shown to be a valid candidate [9, 94]. The WK filter is simply the cross-correlation between the input signal and the spike train over the power spectrum of the input signal

$$h = \int_{-f_c}^{f_c} df \frac{S_{sx}(-f)}{S_{xx}(f)}, \tag{5.2}$$

where f_c is the cut-off frequency of the stimulus, $S_{sx}(-f)$ is the Fourier transform of the cross-correlation between stimulus and spike train and $S_{xx}(f)$ is the Fourier transform of the autocorrelation of the spike train. When convolved with the spike train, this filter will provide an estimate of the input signal which can then be used to obtain a quantifiable measure of information transmission. A typical example of what a WK filter looks like can be seen in Figure 5.2.

Applying this methodology to a single spiking neuron is a very straightforward task. The neuron is presented with a stimulus which for the purposes of illustration is one that induces a vivid neural response. It goes without saying that attempting to construct a linear stimulus reconstruction filter based on the activity, or rather inactivity, of a silent neuron, would prove to be a fruitless task. In fact, there is an optimum number of spikes and also length of stimulus presentation time for the purposes of filter calculation but that depends on the system and setup at

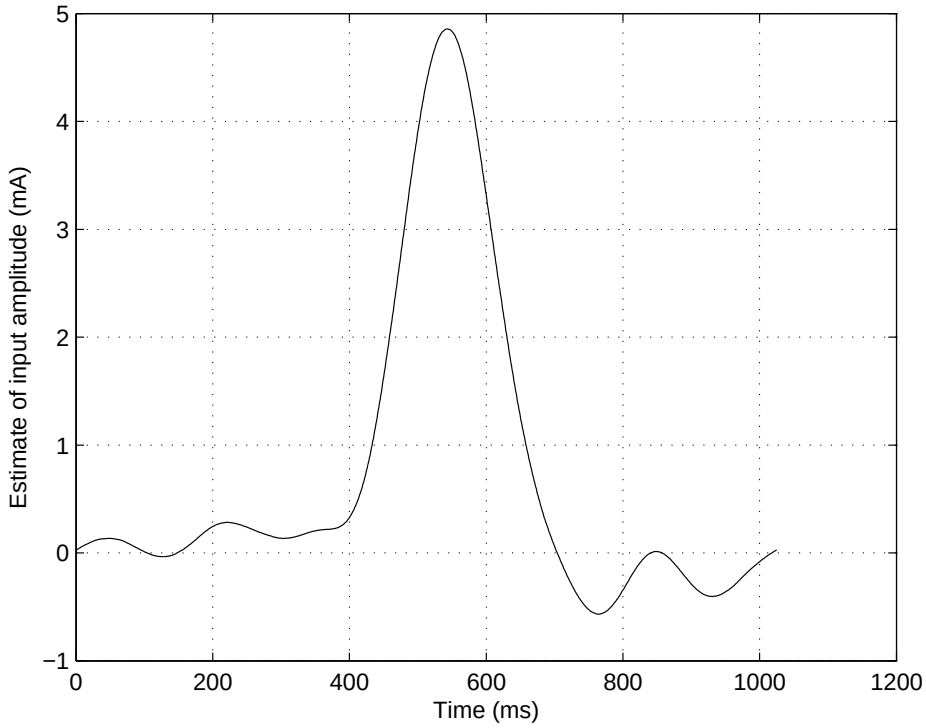

Figure 5.2: *A Wiener-Kolmogorov filter for stimulus estimation of a single neuron. This is a characteristic example of what a WK filter looks like when the Izhikevich spiking neuron model is presented with continuous analogue input. This effectively demonstrates what can be predicted about the input at a specific point in time given a single spike in the neural response.*

hand. The power spectrum of the stimulus is calculated and also the cross-correlation between stimulus and neural response. The cross-correlation divided by the stimulus power spectrum can then be convolved with the spike train and produce an estimate of the stimulus (see Figure 5.3). This, of course, is a simplified version of the entire process. In truth, calculating a WK filter is a more detailed task.

It quickly becomes obvious, however, that this is a very efficient, if slightly tasking, method for estimating the input of a spiking neuron and therefore it constitutes a very good first step in designing an online noise optimisation framework for spiking neurons.

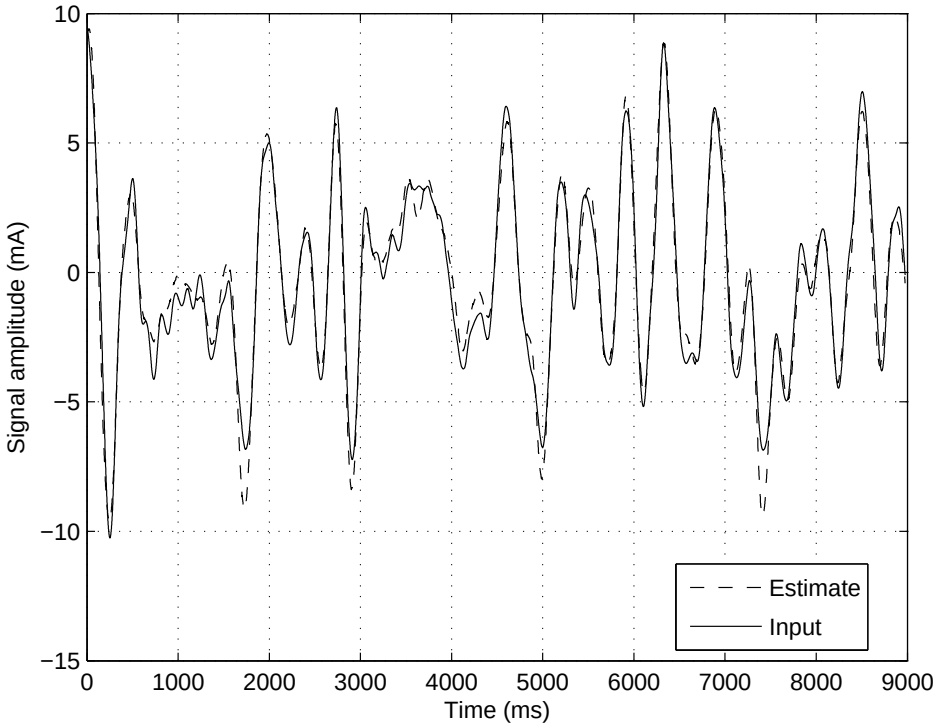

Figure 5.3: *Stimulus reconstruction for a single Izhikevich neuron. In the specific case of an individual neuron, filter-aided input signal reconstruction can be very accurate, as in this example, reconstructing accurately more than 90% of the input signal. In this example, we can see the input signal and its estimate differing only slightly at certain points in amplitude whereas the temporal character of the stimulus is preserved almost perfectly.*

5.6 Optimisation algorithm for a single spiking neuron

Based on the results obtained on stimulus reconstruction and consequently information transmission using a WK filter, we can now start to formulate an approach for optimising a spiking neuron with respect to noise level. Stimulus reconstruction has a great degree of accuracy in the specific case of an individual neuron and this can be seen in Figure 5.3.

5.6.1 Algorithm formulation

The noise level optimisation algorithm has two phases resembling those of training and evaluation. In the first phase, the neuron is provided with input for a specific amount of time. The length of this phase is determined by the amount of neural activity produced. Because a certain

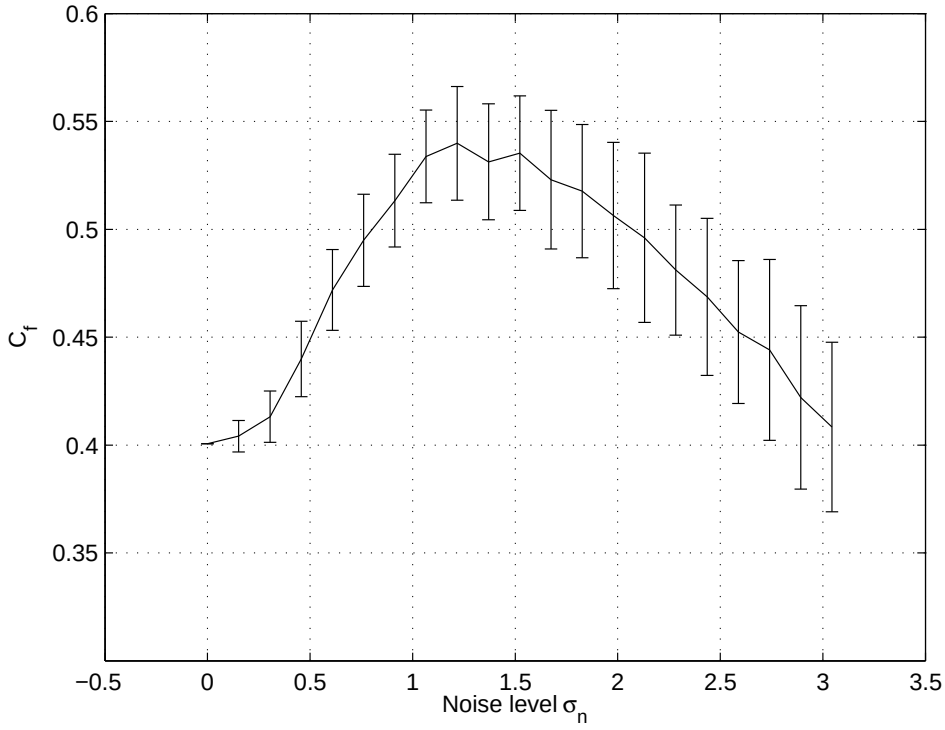

Figure 5.4: *Stochastic resonance in the coding fraction of a single spiking neuron. Stimulus reconstruction under the influence of varying noise amplitude demonstrates an optimum noise level which maximises information transmission through the spiking neuron. These results were obtained by averaging the behaviour of 50 individual Izhikevich neurons. The noise amplitude is measured in standard deviations of the input amplitude.*

amount of spikes is required in order for the WK filter to provide an accurate estimate, another determining factor on the length of this phase is the input amplitude and its characteristics in general. In this set of experiments 500 spikes where enough but the exact number depends on the statistics of the input observed by the neural system. In the case of an individual neuron and with an input ranging between $-10mA$ and $10mA$ (see Figure 5.3), the prerequisite number of spikes is acquired within a $10s$ time window. This is also important in order for the algorithm to be online. Shaping the WK filter adequately will make it useful as an estimator in cases where nothing is known about the input. However, the filter runs the risk of being under- or overfitted. Too few spikes and the filter provides an inaccurate estimate of the input, too many and when it is used to reconstruct an unknown input signal it fails.

In the second or evaluation phase, the WK filter produced earlier is used to reconstruct the input

lacking any knowledge about its characteristics. The only given in this case is the neuron's activity. For the purpose of simplicity and illustration, this part of the algorithm was initially formulated as simple gradient ascent

$$\sigma_n' = \gamma sgn(\Delta C_f), \tag{5.3}$$

where σ_n is the neuron's noise amplitude, γ is the learning rate (with a value of 0.1), ΔC_f is the gradient of the coding fraction and the signum function is used to make the optimisation process more robust.

The coding fraction is a quantity related to the mutual information and equivalent in the sense that it too measures the amount of information that is common between the input and the output signal of the system under study. It is defined as

$$C_f = 1 - \frac{\sqrt{MSE(s - s_{est})}}{\sigma_s}, \tag{5.4}$$

where $\sqrt{MSE(s - s_{est})}$ is the square root of the mean-square error between the input signal and its estimate provided by the WK filter. This quantity is normalised by the standard deviation of the input σ_s and then is inverted. The coding fraction can theoretically take values between 0 and 1 where 0 signifies that input signal estimation is as good as a random guess and 1 signifies a perfect reconstruction of the input signal.

5.6.2 Results

The notion that forms the basis of this approach can be seen in Figure 5.1. What is essentially a measure of distance between the signal that was presented as input to the neuron and the estimate of the signal produced using a WK filter and the neuron's spike train, gives us an adequately accurate and computationally cost-effective estimate of information transmission.

For the scope of this research, adequacy in terms of accuracy is considered to be achieved when well known phenomena, such as stochastic resonance, are reproduced consistently and with a degree of accuracy comparable to that of more detailed, analytical approaches. In other words, this approach will certainly not provide insight as accurate as statistical analysis but as long as it depicts the same mechanisms and information dynamics, it is good enough to use as the basis

of an optimisation framework (see Figure 5.4).

The standard version of the gradient ascent algorithm, however simple and elegant, falls short of being a reliably effective approach to optimising the neuron's noise level. This is not, however, due to some inherent inefficiency of the algorithm. Rather, it is because of the nature of the coding fraction and the search-space it describes. In an attempt to increase the algorithm's reliability, momentum and annealing where applied to the gradient ascent approach, first in turn and then together. Neither improved the algorithm much.

Finally, a more conservative yet effective approach was used. A more cautious version of gradient ascent in which a change in the noise level is made only if it will lead to a positive change in the coding fraction and consequently in information transmission. This means that the algorithm calculates the effect a change in the noise amplitude would have on the coding fraction and that this change is only made if it would improve the coding fraction. This approach provided much better results than the previous ones. It is also reliable and robust enough to be used as a simple optimisation method for the noise level of a spiking neuron.

$$\sigma_n' = \gamma sgn(\Delta C_f), \tag{5.5}$$

The main goal of this part of the approach is to provide proof of concept. To demonstrate that simple algorithms can be designed that optimise the noise level in neural systems with respect to information transmission and processing capabilities and that it is possible for this to happen online. In a very concrete sense, this is exactly what this approach achieves.

Figure 5.5 shows a characteristic example of online noise amplitude optimisation in a single neuron. The algorithm can get trapped in local optima for several epochs but eventually it escapes them. In Figure 5.6 is the evolution of the coding fraction during noise optimisation as seen in Figure 5.5. The coding fraction describes a very noisy and rough search-space with a multitude of local optima. This is understandable since only one set of data was used to estimate information transmission.

This set of results demonstrates something more than an algorithm for online noise level optimisation for spiking neurons. It serves as a proof of concept for the fact that online noise optimisation is feasible on the individual neuron level. What this means is that even though to fully comprehend the intricate dynamics of information in a neural system detailed statistical

analysis is needed, optimising these very dynamics, however roughly, may be much easier than previously thought.

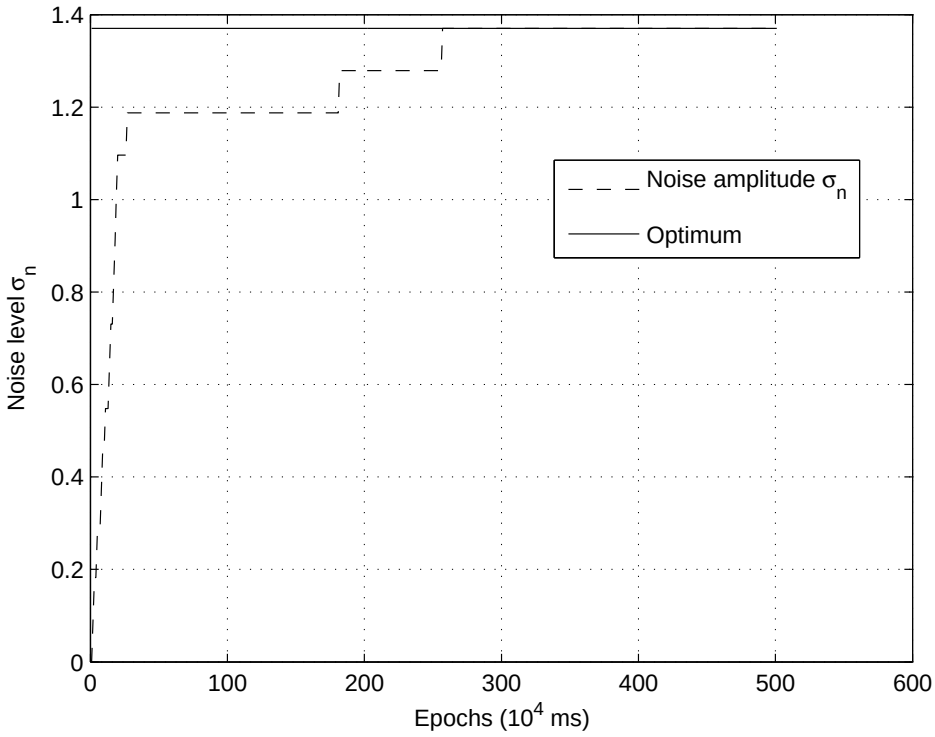

Figure 5.5: *Noise amplitude during optimisation. The noise amplitude optimum depicted here as a solid line is determined during a preliminary phase during which everything is held constant apart from the noise level and every point is determined and averaged over 50 runs, very much like in Figure 5.4. An initial and rapid increase in noise amplitude brings it very close to the optimum and the optimum is reached several epochs later. In cases such as this one, the algorithm might get trapped in local optima for some epochs. This is most likely due to the roughness of the search space (see Figure 5.6).*

5.7 Extending the algorithm for a neural population

The next obvious, logical step is attempting to extend this methodology to more complicated neural systems. Online optimisation of noise in a single spiking neuron is no small feat but the possibility of a neural population being able to regulate its own noise level via some mechanism in a biologically plausible framework is undeniably significant.

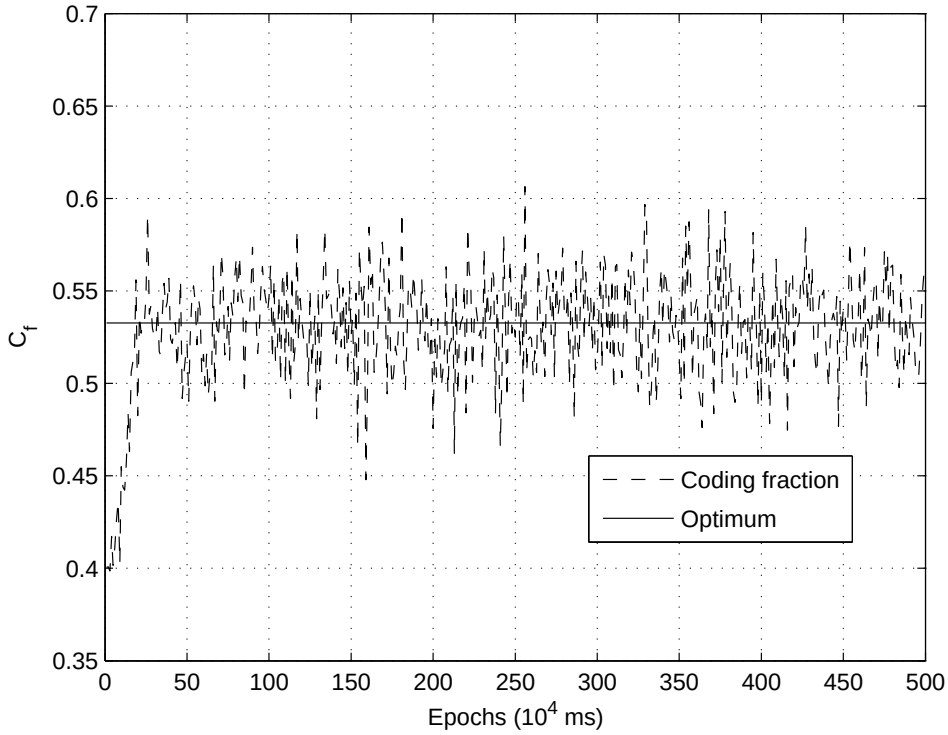

Figure 5.6: *Coding fraction during optimisation. This result is from the same experiment as the one that produced Figure 5.5. Here it becomes obvious that the initial jump in noise amplitude seen in Figure 5.5 brought the coding fraction, and consequently information transmission, very close to the optimum.*

5.7.1 Algorithm formulation

In the case of a population of spiking neurons, employing a noise optimisation method such as the one mentioned above may not be as straightforward as it first appears. Since the approach being used has its roots in the field of signal processing and the neural population is treated as a signal processing and transmission system, each signal must be clearly defined and justified. In the case of a single input single output neural population, it is fairly easy and intuitive which signals will be the input and output signal. The signal presented to the single input neuron is the input signal for the purposes of this approach and the output neuron's spike train is the output signal.

This choice, however, becomes harder when dealing with a neural population with multiple inputs or multiple outputs or both. In this case, choosing which signals, and which of their combinations, represent input and output can be hard and occasionally may seem entirely arbi-

trary. For example, the spike trains of the output neurons could be considered to be the neural population's response but then there is the question of their representation. Are their spike trains to be treated as an array of signals? Or is it justified to use their pooled activity which is simply an addition of the signals? Is representing each group activity instance as a value in a digital but no longer binary signal a possible approach?

All of the above are valid questions which any researcher has to face, answer and justify. They can all be valid and justifiable answers and choosing one of them may seem arbitrary. In this particular case, the pooled activity of the network is used as the output signal. This is consistent with our approach taken in calculating various information theoretic measures. It is also a biologically plausible approach and it also simplifies the numerical aspect of this methodology greatly without compromising the conclusions drawn.

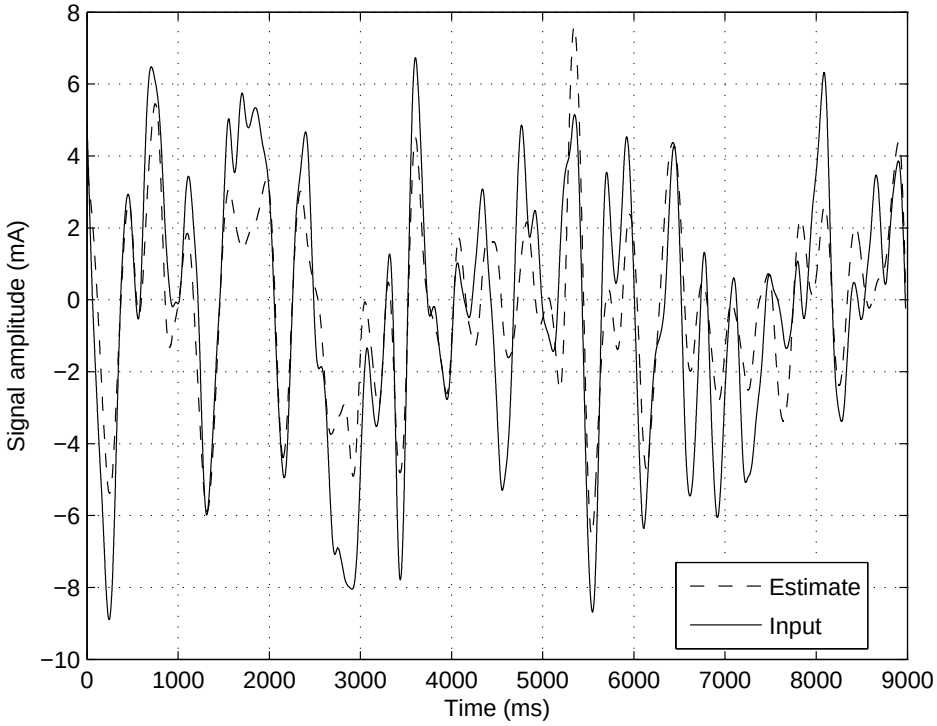

Figure 5.7: *Stimulus reconstruction for a population of Izhikevich neurons. In the case of neural populations, filter-aided input signal reconstruction can also be very accurate. Signal reconstructing can reach above 90% accuracy. The input signal and its estimate differ only slightly at certain points in amplitude and in a greater degree than in the case of an individual neuron, whereas the temporal character of the stimulus is preserved almost perfectly.*

Of course, this is not the only issue in this case. There is no good reason why the entire neural population's response cannot be considered to be the output signal, especially if the network is one with recurrent and lateral synaptic connections. This makes hierarchical boundaries fuzzier and could mean that choosing any subgroup of neurons as the output neurons could very well be an arbitrary decision. As far as the input is considered, when multiple input neurons are presented with the same input deciding what the input signal is can be relatively easy. The same is not true for multiple, different input signals. In this case, as in the case of the output signal, one has to choose between a variety of options and be able to justify their choice.

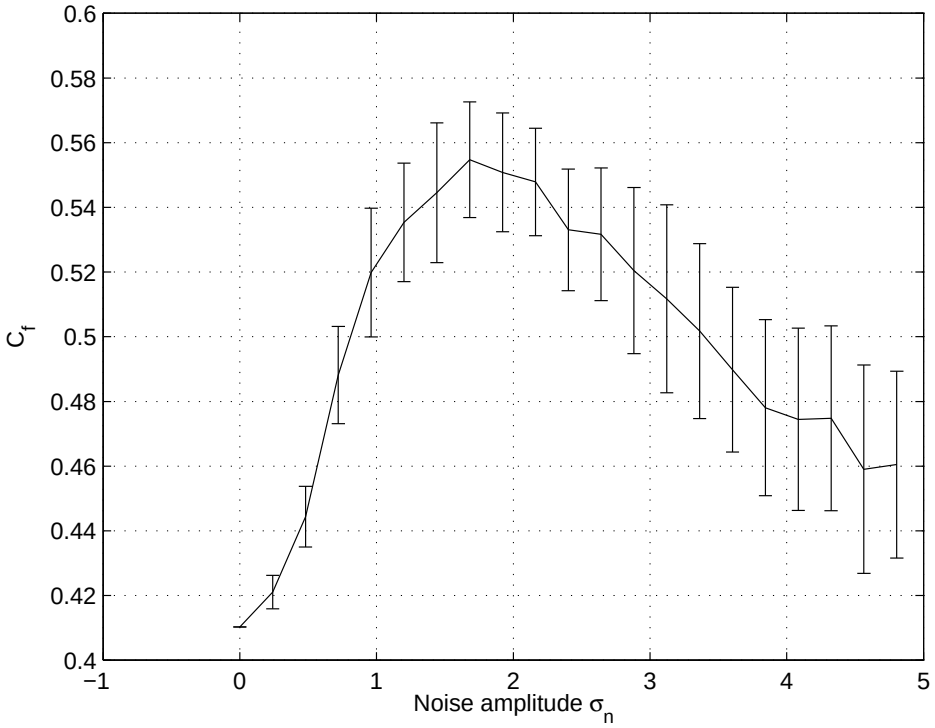

Figure 5.8: *Stochastic resonance in the coding fraction of a neural population. Stimulus reconstruction under the influence of varying noise amplitude demonstrates an optimum noise level which maximises information transmission through the population of spiking neurons. These results were obtained by averaging the behaviour of 100 feedforward spiking neural networks with similar connectivities and architectures. The noise amplitude is measured in standard deviations of the input amplitude.*

In the case of a neural population the output signal was considered to be the activity of the entire population. This choice was made for two reasons. Firstly, because any other method would ignore the activity of some group of neurons and also because unless there is a rigid and well

defined architecture with a distinct output layer, choosing a group of neurons as output neurons seems like an arbitrary choice. Consequently, in order to have a comprehensive perspective as to what is happening in the network as a whole and one that can be generalised to other populations and will not be over-specific, pooling the activity of all the neurons together seemed to be the wisest choice.

The methodology studied above presents yet another difficult choice. Should the neural population be treated as a singular information processing and transmission entity or can the neurons be treated and therefore optimised individually while still interconnected in a functioning neural ensemble? In this set of experiments neural activity was pooled, as mentioned above, in order to treat the network as a single information transmission and processing channel and also to simplify numerical analysis and lower computational cost. More importantly however, this approach was chosen in order to avoid "black-boxing" the network's internal activity while still maintaining the ability to optimise the neural population online as a whole and with a single parameter.

The network version of the online noise level optimisation algorithm is very similar in its formulation to the single neuron version.

$$\sigma'_N = \gamma sgn(\Delta C_f), \tag{5.6}$$

where σ_N is the noise amplitude of all the neurons in the network controlled with a single universal parameter, γ is the learning rate, ΔC_f is the gradient of the coding fraction and the signum function is used to make the optimisation process more robust.

In this case, the coding fraction is the same quantity related to the mutual information as mentioned above but with a significant difference. It is defined as

$$C_f = 1 - \frac{\sqrt{MSE(S - S_{est})}}{\sigma_S}, \tag{5.7}$$

where $\sqrt{MSE(S - S_{est})}$ is the square root of the mean-square error between the input signal and its estimate provided by the WK filter. In this case however, the signal estimate is produced by treating the pooled network activity as an output signal. This quantity is normalised by the standard deviation of the network's input σ_S and then inverted.

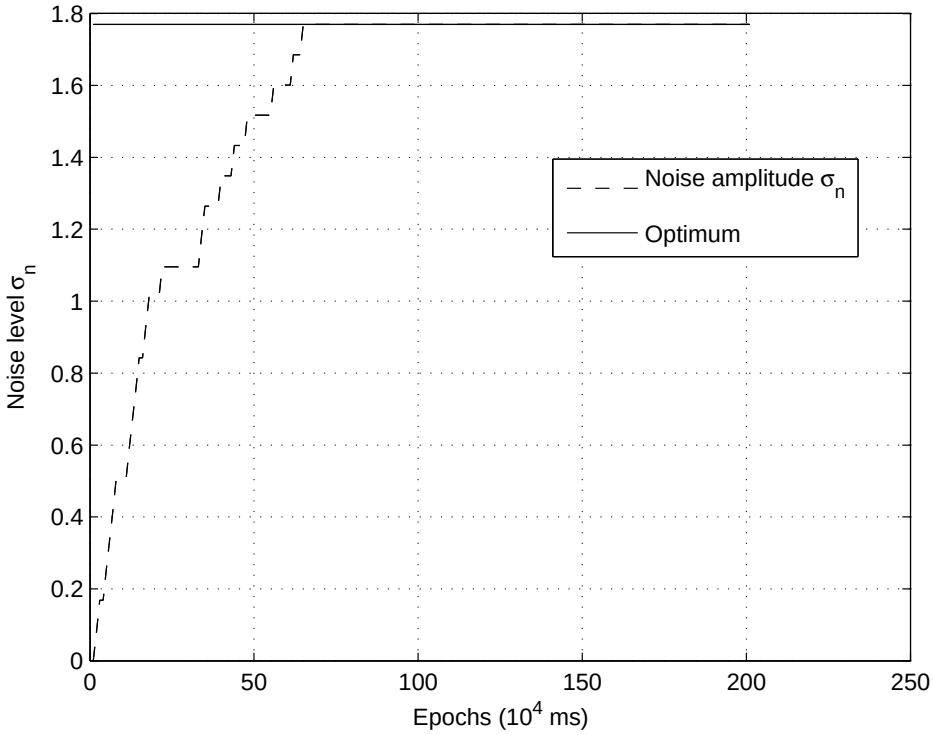

Figure 5.9: *Noise amplitude during optimisation for a neural population. The noise amplitude optimum is shown as a solid line. Every point is determined and averaged over 100 networks of similar architectures and connectivities. This is a characteristic example of online noise amplitude optimisation for an entire spiking neuron population.*

5.7.2 Results

Extending this approach to an entire neural population has provided very positive results. Although not a terribly elegant approach it consistently converges to noise levels that provide optimal information transmission through the network (see Figures 5.9 and 5.10). It provides concrete proof that online noise optimisation in neural systems is feasible and that information theoretic measures can be accurately approximated in order to form the basis of such optimisation attempts. In all the following experiments the neural populations have 100 neurons. All synaptic connections are time-delayed with the time-delays being uniformly distributed between 1 and $4ms$. Connectivity in all the neural populations used in this set of experiments is 20% for all kinds of connections, feedforward, lateral and recurrent. The connection weights are uniformly distributed from 0 to 20.

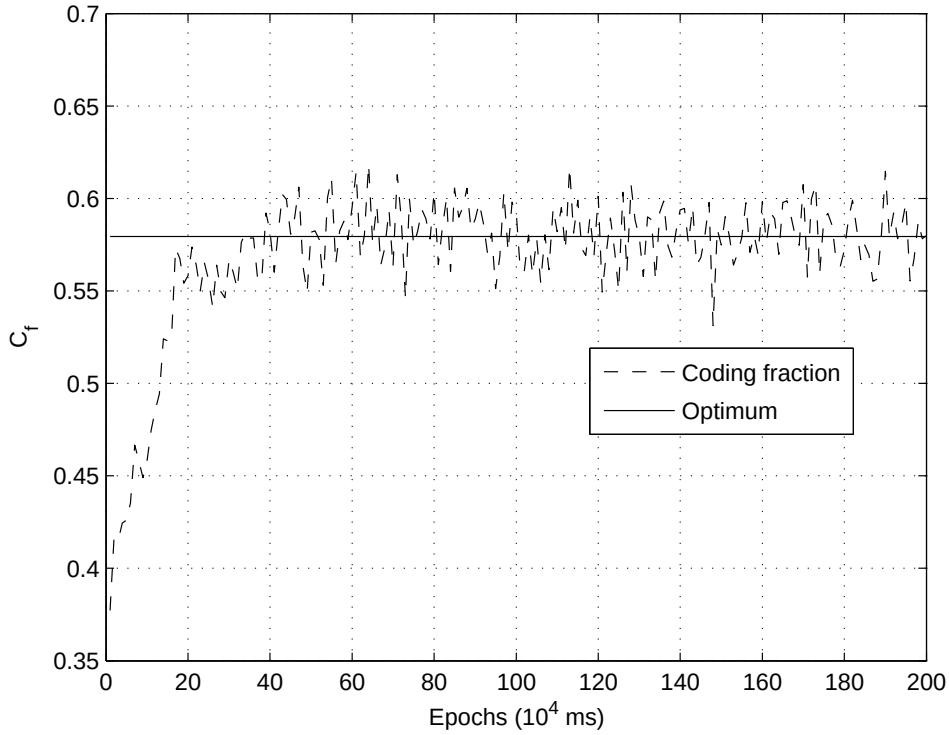

Figure 5.10: *Coding fraction during optimisation for a population of spiking neurons. This result is from the same experiment as the one that produced Figure 5.9. Here too, as in the case of the individual neuron, near optimal coding fraction is reached before optimum noise amplitude.*

These results (Figures 5.9 and 5.10) together with the results obtained by optimising a single neuron (Figures 5.5 and 5.6) show that not only neural systems can be optimised regardless of size and complexity but also that similar principles can be used to optimise them.

Careful observation of the results showing the evolution of the coding fraction of the spiking neural network and that of the noise amplitude (Figures 5.9 and 5.10) and those showing the effect of noise amplitude on information transmission (Figure 5.8) paints an interesting picture. For the optimum noise level and close to that point on either side the coding fraction does not change much with a change in noise amplitude. This demonstrates that neural systems have a certain tolerance to noise level changes close to their optimum with respect to information transmission.

On the other hand, the further away the noise level is from the optimum any change in it has more significant effects on information transmission, and consequently information processing,

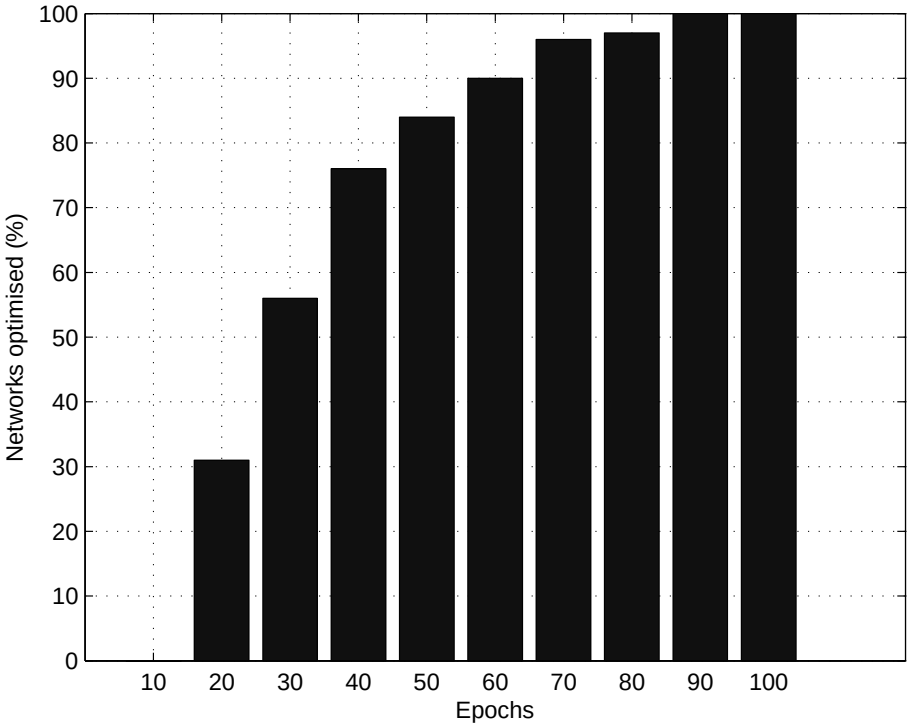

Figure 5.11: *Optimisation algorithm convergence. This shows the effectiveness of the optimisation algorithm. Each bar represents the percentage of networks optimised with respect to noise after a certain number of epochs have passed. By epoch 90 all networks have been optimised. To obtain this result 100 different spiking neural networks were used.*

whether that is constructive or destructive. This phenomenon could potentially be used to design a more effective optimisation methodology and perhaps provide a link with biological networks. Put more simply, a more efficient optimisation algorithm could take advantage of the phenomenon observed above and make quick, effective changes in noise levels while avoiding costly fine tuning.

A visualisation of just how effective this optimisation algorithm is can be seen in Figure 5.11. A large proportion of the networks are optimised very quickly and by epoch 90 all of the networks have been optimised. This is an exciting, positive result but it should also be kept in mind that each epoch is $10s$ long. This means that optimisation for a spiking neural network using this algorithm can take anywhere from 1 to 15 minutes simulation time. In the meantime, the input signal could have changed in terms of statistics several times. This approach is an excellent

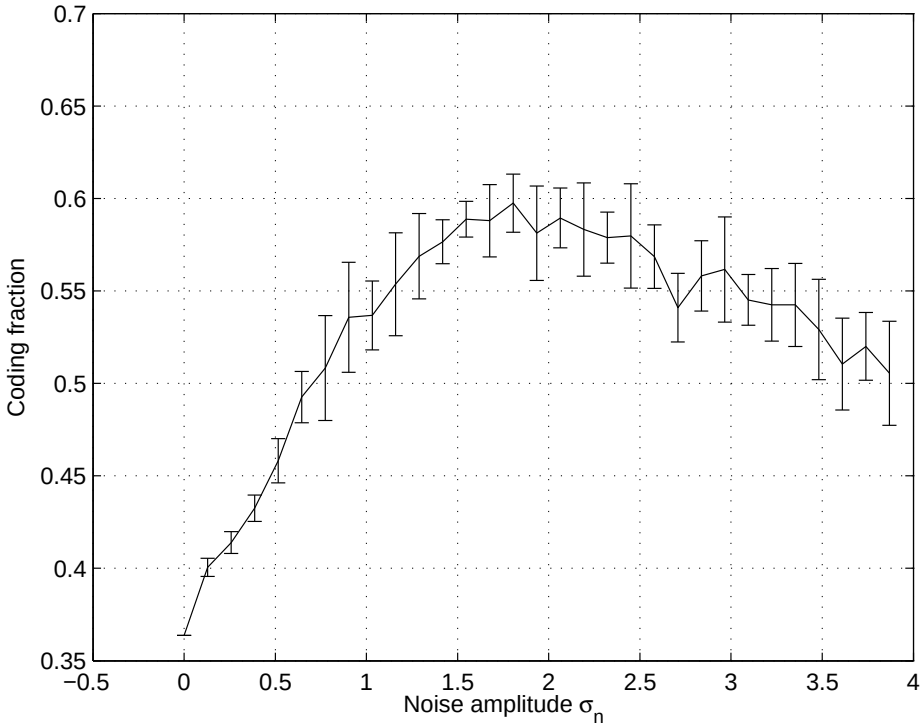

Figure 5.12: *Stochastic resonance in spiking neural networks with lateral connections. Clearly the phenomenon of stochastic resonance is a widespread one and one that can be optimised in a variety of systems. In this case, 100 feedforward spiking neural networks with lateral connections were averaged in order to obtain this result.*

first step but it is definitely not exhaustive.

By adding features in the network's architecture it can be verified that there are mechanisms and phenomena that can be exploited in order to optimise the information processing capabilities of the neural population as a system. It can also be shown that the algorithm and the framework as a whole is truly generalisable and extendible. To illustrate this, lateral connections were added to the feedforward networks previously used. It becomes obvious that stochastic resonance is a characteristic phenomenon of neural systems (see Figure 5.12). Its shape changes, indicating a different response to changes in noise amplitude but otherwise it is a typical SR signature.

This also demonstrates another interesting concept and that is the fact that structural changes affect the system's response to noise. The most important difference between the stochastic resonance signatures of feedforward spiking neural networks with and without lateral connections (see Figure 5.12 and Figure 5.8 respectively), is a change in the steepness of the slope with the

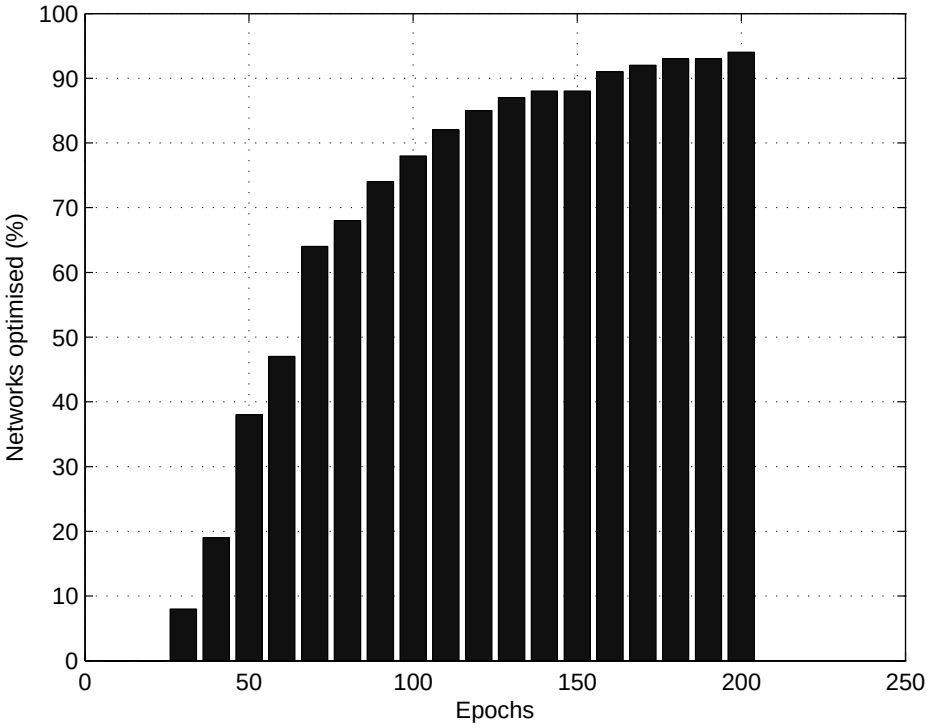

Figure 5.13: *The effectiveness of the algorithm with feedforward networks with lateral connections. In this case too, each bar represents the percentage of networks optimised by a certain epoch. However, the addition of lateral connections in the networks translates into slower convergence of the algorithm. Here, by epoch 200 roughly 95% of the networks have optimised their noise.*

addition of the lateral connections. This is an indication that perhaps lateral connectivity in a network adds a certain element of stability and resistance to changes due to noise.

As far as algorithm efficiency goes, adding lateral connections to the network appears to have negative consequences (see Figure 5.13). Convergence is much slower in this case, taking in some cases more than double the number of epochs to achieve a comparable coding fraction as in Figure 5.12. This could be caused by the same underlying mechanism that causes the reduction in steepness on the slopes of the SR response in the coding fraction. It could be the case that it is harder, on average, to optimise a network with lateral connections with respect to noise because lateral connectivity introduces a certain resistance to changes due to noise.

Adding recurrent connections in a feedforward spiking neural network with lateral connections causes even more changes in the network's response with respect to noise. The coding fraction

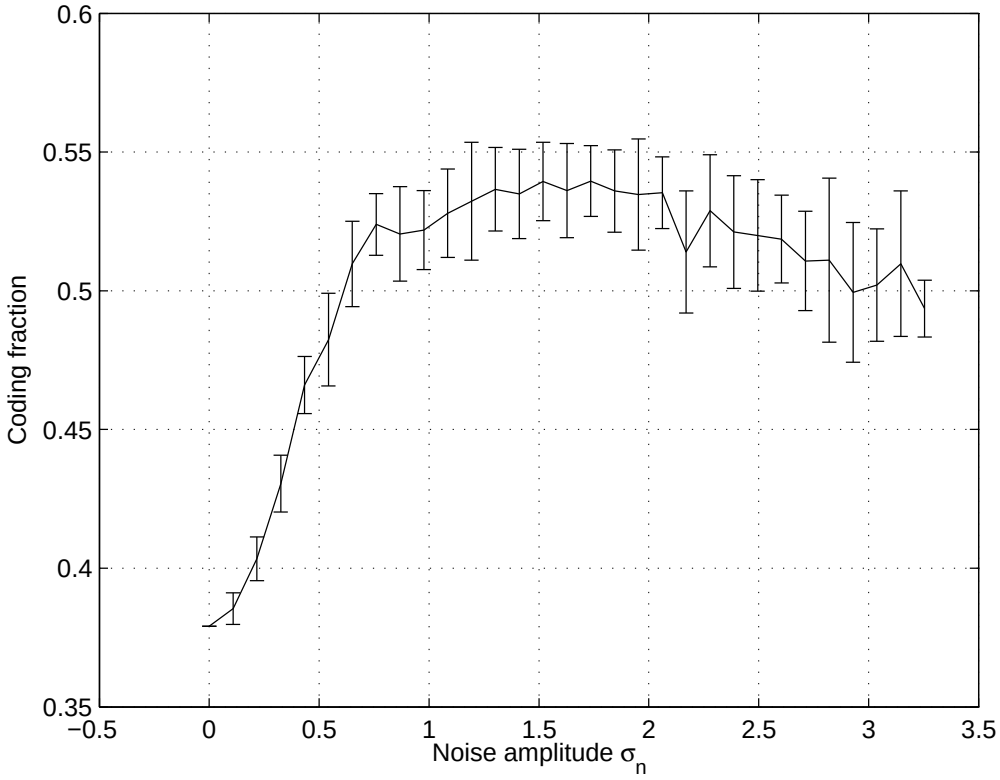

Figure 5.14: *Stochastic resonance in spiking neural networks with lateral and recurrent connections. In this case too, 100 spiking neural networks with lateral and recurrent connections were averaged in order to obtain this result. Stochastic resonance can be observed in this case too, the only difference being a much slower drop in information transfer with increasing noise past the noise optimum.*

increases with increasing noise similarly to all other architectures mentioned above until it reaches the noise optimum. After that, any increase in noise seems to have minimal effect on the network's information transmission (see Figure 5.14). In other words, adding recurrent connections in a spiking neural network with lateral connections maintains the constructive effect of noise but also manages to minimise its destructive aspects.

The addition of recurrent connectivity has more than one positive effects with respect to noise. Apart from minimising the destructive effects of noise on information transmission, it also speeds up optimisation of noise levels (see Figure 5.15). The speed up is such that not only does it counteract the slowing down by the addition of lateral connectivity but it also makes noise

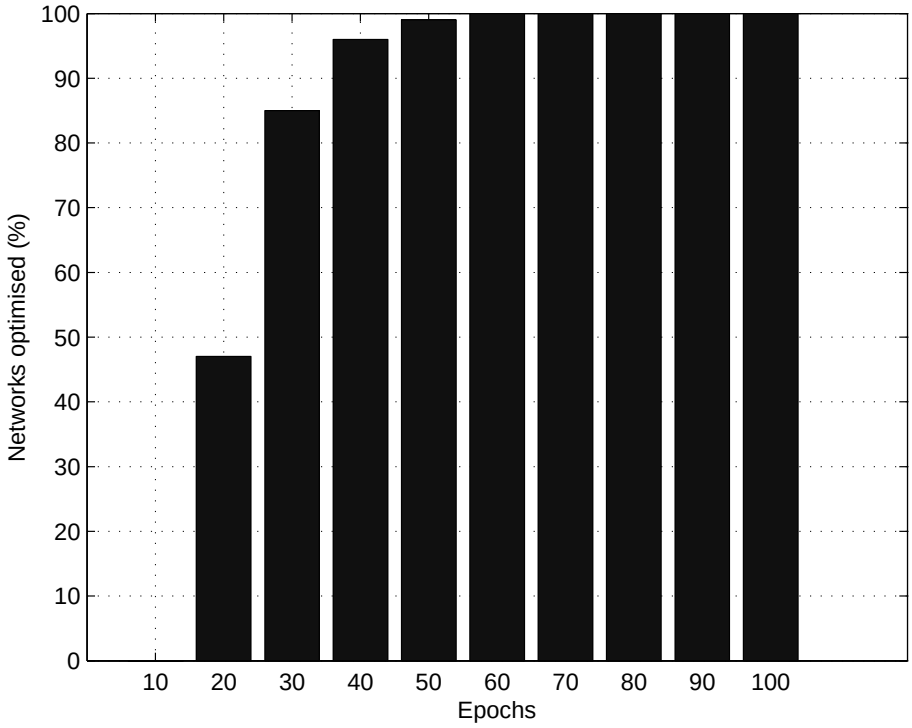

Figure 5.15: *The effectiveness of the algorithm with feedforward networks with lateral and recurrent connections. Each bar represents the percentage of networks optimised by a certain epoch. The addition of recurrent connections in the networks seems to counteract the effect of lateral connections seen in Figures 5.12 and 5.13. In this case, all of the networks have been optimised by epoch 60, making convergence faster than feedforward networks with or without lateral connections.*

optimisation faster than in the case of the simple feedforward network. This is further evidence that structure and architecture plays an important role even in the case of noise optimisation.

These additions in connectivity and architecture were made mainly to illustrate a point and that is that architecture is important when it comes to optimising the effects of noise. It should be taken into account when designing an algorithm for noise optimisation and it certainly needs to be taken into account when judging an optimisation method's efficiency. Studying the effects of connectivity and other aspects of structure, such as time delays, can provide valuable insight into information dynamics and how they are affected by changes in noise.

5.8 Summary

Mutual information was used as the foundation for a more appropriate measure and as the starting point for a methodology that would allow the online optimisation of a neural system. The connection between mutual information and mean square error was presented and stimulus estimation was detailed as a viable candidate for online noise optimisation. An algorithm for online noise optimisation in a single neuron was formulated and the successful results were presented. The algorithm was extended and applied to various neural populations with similar success.

Chapter 6
Conclusions

Stochasticity is a large chapter on how neural systems work. Whether one's goal is to devise an optimisation methodology for artificial spiking neural networks or to understand how biological neural networks could have evolved to take advantage of their surrounding stochasticity and what effects it has on their computational capabilities, this area of research poses interesting questions about how neural systems work. Noise is not only the obvious randomness of a signal. It is the reliability, or lack thereof, of timing in the neural response. It is the insertion or deletion of information from the system's activity and it is the apparent chaoticity in a neuron's or a network's behaviour. In essence, it is also a resource. It is free energy flowing around and through the neural system.

Designing systems that will take advantage of this free-flowing energy is desirable not only from the engineering point of view, that is designing elegant and efficient systems, but also because it provides a link with neuroscience in terms of understanding and elucidating underlying principles of stochasticity and its manipulation in neural systems.

The main hypothesis in this work is that noise can and does have a positive effect on certain aspects of a spiking neural system's behaviour, that these effects are generalisable and that they are exploitable by the neural systems themselves. Also, this work intended to show that positive stochastic phenomena can be exploited online and in a biologically plausible way.

Establishing that certain stochastic phenomena also occur in complex populations of biologically inspired spiking neurons is an integral part of this work. However, optimisation with respect to noise is elusive. In this work, determining an optimum for noise was not enough. The effect of noise on information transmission had to be expressed in such a way that optimisation was made meaningful and potentially biologically accurate. More importantly, the positive effects of noise were expressed in such a way that the neural system could take advantage of them immediately and efficiently.

6.1 Noise

From the very first set of results, this work verified the now established notion that noise is not necessarily a destructive force in neural systems. Phenomena like Stochastic Resonance are observed in a multitude of systems and in a variety of circumstances (see Figures 3.4, 4.2, 5.4, 5.8, 5.12 and 5.14). This demonstrates clearly that noise can have a positive effect on certain aspects of neural systems and, in this particular case, on information transmission.

6.2 Information theory

Using Information Theory for the study of neural behaviour proved to be a wise choice because it provides the researcher with a wide array of tools for a variety of different approaches. Measures and quantities such as entropy and mutual information which are based on statistical analysis provide a solid background on the effects of noise on information dynamics and processing. On the other hand, less computationally expensive measures based on approximations or notional equivalents of information theoretic measures can be used to manipulate certain phenomena or effects after they have been shown to exist conclusively via statistical analysis.

Statistical analysis was used in this case to study the effect of intracellular noise on the behaviour of single neurons and larger neural populations. More particularly, detailed analysis of the effect of noise amplitude on information transmission was carried out. This was done in order to establish equivalence and relevance with other examples of information transmission under the influence of noise. It was also done in order to verify the fact that noise has a constructive effect on the information transmission capabilities of neural systems of varying sizes and structure (see Figures 3.4, 4.2, 5.4, 5.8, 5.12 and 5.14).

6.3 Neural systems

The results collected in this series of experiments also highlighted something important. Noise resistance or even exploitation may not be an extrinsic, top-down process. It may very well be an intrinsic property at any level of organisation in a neural system, be it a property of an ion channel, the behaviour of a single neuron, a structural characteristic of the neural ensemble or any combination of the above. This may have implications on the way spiking neuron models are designed or the kind of network architectures that are used in real world problems. One

thing is certain however and it is that neurons and their networks have evolved in a noisy environment. Consequently, it is safe to assume that certain properties may have evolved that allow resistance to or even exploitation of the chaoticity that surrounds them.

6.4 Optimisation

Identifying positive stochastic phenomena forms the basis of any attempt at optimisation. Unfortunately, the methodology that allows the elucidation and study of information dynamics under the influence of noise is not an appropriate framework for optimisation. Statistical analysis requires data collected from several identical runs where everything is kept constant apart from the intracellular noise. A paradigm such as this bears no relevance to biology. Input signals and a multitude of other parameters change rapidly and a neural system must keep up with them. Consequently, detailed statistical analysis, although a very powerful tool, is inappropriate for the development of an optimisation framework for any complex neural system.

However, Information Theory can provide an intermediate step in the process of developing optimisation approaches. After identifying and analysing any stochastic phenomenon it is possible to develop methodologies based on the more accurate tools provided by IT that will form the basis of a more effective optimisation approach. These measures will be less accurate but will still be valid approximations of the original statistical quantities, such as entropy and mutual information. More importantly they will be much less taxing in terms of computation costs.

The above notion was the guiding principle in most of the work detailed here. Detailed study and analysis of constructive stochastic phenomena was followed by a simplification in the approach used in order to reduce data requirements dramatically while maintaining a certain degree of accuracy. This makes it possible to design online optimisation frameworks for neural systems. Stochastic phenomena can be captured even with only one set of data while still allowing quick and effective optimisation of the noise level (see Chapter 5).

In short and with respect to the possibilities and restrictions of stochastic optimisation, this work shows that IT is a valuable tool-set if used as a starting point for the development of more sophisticated tools. It also shows that online stochastic optimisation is not only feasible but most likely preferable and that this approach is not only more efficient but also, potentially, more biologically plausible.

6.5 Biological plausibility

Another important aspect of this work is how it ties in with neuroscience. Using biology as inspiration is always a useful idea to keep in mind but more important is how these results relate with actual biological processes. Biological neural systems only have one chance at processing the data they receive, that is to say, they cannot collect several sets of data and analyse them statistically. Any kind of statistics about the data they process must either be calculated instantaneously and locally and therefore be inaccurate or some neural subsystems must be tasked with the role of statisticians, collecting data, analysing it and then imposing their conclusions on the rest of the system. The first, option appears more plausible and much more appealing.

This leads to the natural question of how can neural systems achieve this instant analysis. Intuitively, whatever methodology they use must be governed by simple principles such as economy, the less energy spent performing this task the better, and efficiency, that is to say, this effort should provide tangible and substantial results with as low costs as possible. The approach described above as a candidate for online optimisation of noise levels in spiking neural systems agrees perfectly with these principles.

Another possibility, highlighted in this work, is that neural system structure and other specific properties determine the effect of noise in such a way that not much is needed in terms of optimisation. This is a rather important notion since it would mean that neural systems have evolved to exploit stochasticity passively, an approach that would be extremely efficient.

6.6 Future work

However positive these results and conclusions may be, there are aspects of this work that require further study. Developing new tools for the study of neural stochastic dynamics is very important. Not only thorough, analytical tools that will dissect neural systems and their behaviours but also less accurate but effective tools that will allow us to exploit phenomena and behaviours in a tangible and meaningful way.

Another important aspect is the study of this area in biological neural systems. Understanding how biological neural networks approach this problem should prove to be of great value not only because it will allow greater understanding of biological neural systems but because it will

also allow the design of better artificial ones. Linking these two worlds is very important and will have great consequences for both of them.

The possibility that the structural characteristics of a network play an important role in the control of noise and its effects should be investigated. Determining which properties of a neural population affect certain aspects of stochasticity could lead to the development of neural systems which can passively control noise and optimise stochasticity regardless of the environment.

Finally, refining the online optimisation methodology presented here or even finding more efficient alternatives should be pursued as it is the most likely approach to provide us with more powerful information processing neural systems and also a potential link with biological neural systems and their mechanisms.

References

[1] S. R. y Cajal, "Histologie du systeme nerveux de l'homme et des vertebres (french edition reviewed and updated by the author, translated from spanish by l. azoulay).," vol. 1, pp. 1–3, Oxford University Press, 1909, 1911.

[2] J. E. Dowling, *Neurons and Networks: An Introduction to Neuroscience*. Belknap Press, 1992.

[3] P. Dayan and L. F. Abbott, *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*. The MIT Press, 2005.

[4] W. Bair, C. Koch, W. Newsome, and K. Britten, "Power spectrum analysis of bursting cells in area MT in the behaving monkey," *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, vol. 14, pp. 2870–2892, 1994.

[5] B. Hille, *Ionic Channels of Excitable Membranes*. Sinauer Associates, 1992.

[6] E. Kandel, J. Schwartz, and T. Jessell, *Principles of Neural Science*. McGraw-Hill Medical, 2000.

[7] E. Izhikevich, "Simple model of spiking neurons," *Neural Networks, IEEE Transactions on*, vol. 14, pp. 1572, 1569, 2003.

[8] S. Mitaim and B. Kosko, "Adaptive stochastic resonance in noisy neurons based on mutual information," *Neural Networks, IEEE Transactions on*, vol. 15, no. 6, pp. 1526–1540, 2004.

[9] F. Rieke, D. Warland, R. de Ruyter van Steveninck, and W. Bialek, *Spikes: Exploring the Neural Code*. The MIT Press, 1999.

[10] G. Deco and B. Schurmann, "Stochastic resonance in the mutual information between input and output spike trains of noisy central neurons," *Physica D: Nonlinear Phenomena*, vol. 117, pp. 276–282, June 1998.

[11] X. Godivier and F. Chapeau-Blondeau, "Noise-enhanced transmission of spike trains in the neuron," *EPL (Europhysics Letters)*, vol. 35, no. 6, pp. 473–477, 1996.

[12] B. Kosko and S. Mitaim, "Stochastic resonance in noisy threshold neurons," *Neural Networks*, vol. 16, no. 5-6, pp. 755–761, 2003.

[13] A. Patel and B. Kosko, "Stochastic resonance in noisy spiking retinal and sensory neuron models," *Neural Networks*, vol. 18, no. 5-6, pp. 467–478, 2005.

[14] I. Y. Lee, X. Liu, B. Kosko, and C. Zhou, "Nanosignal processing: Stochastic resonance in carbon nanotubes that detect subthreshold signals," *Nano Letters*, vol. 3, pp. 1683–1686, Dec. 2003.

[15] S. F. Traynelis and F. Jaramillo, "Getting the most out of noise in the central nervous system," *Trends in Neurosciences*, vol. 21, pp. 137–145, Apr. 1998.

[16] K. J. Friston and K. E. Stephan, "Free-energy and the brain," *Synthese*, vol. 159, pp. 417–458, Dec. 2007. PMID: 19325932.

[17] A. Patel and B. Kosko, "Error-probability noise benefits in threshold neural signal detection," *Neural Networks*, vol. In Press, Accepted Manuscript, pp. 697–706, 2009.

[18] F. Chapeau-Blondeau and D. Rousseau, "Raising the noise to improve performance in optimal processing," *Journal of Statistical Mechanics: Theory and Experiment*, vol. 2009, no. 01, p. P01003, 2009.

[19] J. Nadal, N. Brunel, and N. Parga, "Nonlinear feedforward networks with stochastic outputs: infomax implies redundancy reduction," *Network: Computation in Neural Systems*, vol. 9, no. 2, p. 207, 1998.

[20] M. C. W. van Rossum, G. G. Turrigiano, and S. B. Nelson, "Fast propagation of firing rates through layered networks of noisy neurons," *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, vol. 22, pp. 1956–66, Mar. 2002.

[21] A. K. Seth, "Noise and the pursuit of complexity: A study in evolutionary robotics," pp. 123–136, Springer-Verlag, 1998.

[22] J. Shin, "Adaptation in spiking neurons based on the noise shaping neural coding hypothesis," *Neural Networks*, vol. 14, pp. 907–919, July 2001.

[23] W. Maass and A. M. Zador, "Dynamic stochastic synapses as computational units," *Neural Comp.*, vol. 11, pp. 903–917, May 1999.

[24] A. Papoulis and S. Pillai, *Probability, Random Variables and Stochastic Processes with Errata Sheet*. McGraw Hill Higher Education, 4th ed., Jan. 2002.

[25] F. Duan, F. Chapeau-Blondeau, and D. Abbott, "Enhancing array stochastic resonance in ensembles of excitable systems," *Journal of Statistical Mechanics: Theory and Experiment*, vol. 2009, no. 08, p. P08017, 2009.

[26] M. D. McDonnell, P. Amblard, and N. G. Stocks, "Stochastic pooling networks," *Journal of Statistical Mechanics: Theory and Experiment*, vol. 2009, no. 01, p. P01012, 2009.

[27] T. Hoch, G. Wenning, and K. Obermayer, "Optimal noise-aided signal transmission through populations of neurons," *Physical Review. E, Statistical, Nonlinear, and Soft Matter Physics*, vol. 68, p. 011911, July 2003. PMID: 12935180.

[28] P. H. E. Tiesinga, J. M. Fellous, J. V. Jos, and T. J. Sejnowski, "Optimal information transfer in synchronized neocortical neurons," *Neurocomputing*, vol. 38-40, pp. 397–402, June 2001.

[29] N. G. Stocks and R. Mannella, "Generic noise-enhanced coding in neuronal arrays," *Physical Review E*, vol. 64, p. 30902, 2001.

[30] W. Bialek, F. Rieke, R. de Ruyter van Steveninck, and D. Warland, "Reading a neural code," *Science*, vol. 252, pp. 1854–1857, June 1991.

[31] E. N. Brown, R. E. Kass, and P. P. Mitra, "Multiple neural spike train data analysis: state-of-the-art and future challenges," *Nat Neurosci*, vol. 7, pp. 456–461, May 2004.

[32] N. M. Fernandes, B. D. L. Pinto, L. O. B. Almeida, J. F. W. Slaets, and R. Kberle, "Recording from two neurons: Second-Order stimulus reconstruction from spike trains and population coding," *Neural Computation*, vol. 0, no. 0, pp. 1–21, 2010.

[33] L. C. Sincich, J. C. Horton, and T. O. Sharpee, "Preserving information in neural transmission," *J. Neurosci.*, vol. 29, pp. 6207–6216, May 2009.

[34] N. Brenner, S. P. Strong, R. Koberle, W. Bialek, and R. R. de Ruyter van Steveninck, "Synergy in a neural code," *Neural Computation*, vol. 12, pp. 1531–1552, July 2000. PMID: 10935917.

[35] A. Pouget, P. Dayan, and R. Zemel, "Information processing with population codes," *Nat Rev Neurosci*, vol. 1, pp. 125–132, Nov. 2000.

[36] E. M. Izhikevich, *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting*. The MIT Press, 2010.

[37] E. Izhikevich, "Which model to use for cortical spiking neurons?," *IEEE Transactions on Neural Networks*, vol. 15, pp. 1063–1070, 2004.

[38] O. Sporns and G. Tononi, "Classes of network connectivity and dynamics," *Complexity*, vol. 7, no. 1, pp. 28–38, 2001.

[39] W. Maass, "Vapnik-Chervonenkis dimension of neural networks," in *The handbook of brain theory and neural networks*, pp. 1000–1003, MIT Press, 1998.

[40] W. Maass, "Networks of spiking neurons: The third generation of neural network models," *Neural Networks*, vol. 10, pp. 1659—1671, 1997.

[41] W. Maass, "On the computational complexity of networks of spiking neurons," *Advances in Neural Information Processing Systems*, vol. 7, pp. 183—190, 1995.

[42] W. Maass, T. Natschlager, and H. Markram, "Real-time computing without stable states: a new framework for neural computation based on perturbations," *Neural Comput.*, vol. 14, no. 11, pp. 2531–2560, 2002.

[43] R. Legenstein and W. Maass, "Edge of chaos and prediction of computational performance for neural circuit models," *Neural Networks*, vol. 20, pp. 323–334, Apr. 2007.

[44] C. Houghton, "Studying spike trains using a van rossum metric with a synapse-like filter," *Journal of Computational Neuroscience*, vol. 26, no. 1, pp. 149–155, 2008.

[45] F. Rieke, D. Warland, and W. Bialek, "Coding efficiency and information rates in sensory neurons," *EPL (Europhysics Letters)*, vol. 22, no. 2, pp. 151–156, 1993.

[46] A. Manwani and C. Koch, "Signal detection in noisy weakly-active dendrites," in *Proceedings of the 1998 conference on Advances in neural information processing systems II*, pp. 132–138, MIT Press, 1999.

[47] J. A. White, J. T. Rubinstein, and A. R. Kay, "Channel noise in neurons," *Trends in Neurosciences*, vol. 23, pp. 131–137, Mar. 2000. PMID: 10675918.

[48] E. Schneidman, B. Freedman, and I. Segev, "Ion channel stochasticity may be critical in determining the reliability and precision of spike timing," *Neural Comput.*, vol. 10, no. 7, pp. 1679–1703, 1998.

[49] H. Markram and M. Tsodyks, "Redistribution of synaptic efficacy between neocortical pyramidal neurons," *Nature*, vol. 382, no. 6594, pp. 807–810, 1996.

[50] N. A. Hessler, A. M. Shirke, and R. Malinow, "The probability of transmitter release at a mammalian central synapse," *Nature*, vol. 366, pp. 569–572, Dec. 1993.

[51] W. Gerstner and W. M. Kistler, *Spiking Neuron Models*. Cambridge University Press, 1 ed., Aug. 2002.

[52] R. C. Hilborn and R. J. Erwin, "Coherence resonance in models of an excitable neuron with noise in both the fast and slow dynamics," *Physics Letters A*, vol. 322, pp. 19–24, Feb. 2004.

[53] W. Bialek and F. Rieke, "Reliability and information transmission in spiking neurons," *Trends in Neurosciences*, vol. 15, no. 11, pp. 428–434, 1992.

[54] P. N. Steinmetz, A. Manwani, and C. Koch, "Variability and coding efficiency of noisy neural spike encoders," *Biosystems*, vol. 62, no. 1-3, pp. 87–97, 2001.

[55] M. van Rossum, B. J. O'Brien, and R. G. Smith, "Effects of noise on the spike timing precision of retinal ganglion cells," *J Neurophysiol*, vol. 89, pp. 2406–2419, May 2003.

[56] A. F. Murray and P. J. Edwards, "Synaptic weight noise during MLP learning enhances Fault-Tolerance, generalization and learning trajectory," in *Advances in Neural Information Processing Systems 5, [NIPS Conference]*, pp. 491–498, Morgan Kaufmann Publishers Inc., 1993.

[57] T. Natschlager and W. Maass, "Dynamics of information and emergent computation in generic neural microcircuit models," *Neural Networks*, vol. 18, pp. 1301–1308, Dec. 2005.

[58] M. C. W. van Rossum and A. Renart, "Computation with populations codes in layered networks of integrate-and-fire neurons," *Neurocomputing*, vol. 58-60, pp. 265–270, June 2004.

[59] W. Maass, "Lower bounds for the computational power of networks of spiking neurons," *Neural Comput.*, vol. 8, no. 1, pp. 1–40, 1996.

[60] E. Korutcheva, N. Parga, and J. Nadal, "Information processing by a noisy binary channel," *Network: Computation in Neural Systems*, vol. 8, no. 4, p. 405, 1997.

[61] W. Maass, "Noisy spiking neurons with temporal coding have more computational power than sigmoidal neurons," *Advances in Neural Information Processing Systems 9*, vol. 9, pp. 211—217, 1997.

[62] H. G. Schuster, "Learning by maximizing the information transfer through nonlinear noisy neurons and "noise breakdown"," *Physical Review A*, vol. 46, no. 4, p. 2131, 1992.

[63] S. Wu, W. Ren, K. He, and Z. Huang, "Burst and coherence resonance in Rose-Hindmarsh model induced by additive noise," *Physics Letters A*, vol. 279, no. 5-6, pp. 347–354, 2001.

[64] R. D. R. V. Steveninck and W. Bialek, "Real-Time performance of a Movement-Sensitive neuron in the blowfly visual system: Coding and information transfer in short spike sequences," *Proceedings of the Royal Society of London. Series B. Biological Sciences*, vol. 234, no. 1277, pp. 379–414, 1988.

[65] E. Schneidman, S. Still, M. J. Berry, and W. Bialek, "Network information and connected correlations," *Physical Review Letters*, vol. 91, p. 238701, Dec. 2003.

[66] D. P. Feldman, C. S. McTague, and J. P. Crutchfield, "The organization of intrinsic computation: Complexity-entropy diagrams and the diversity of natural information processing," *Chaos: An Interdisciplinary Journal of Nonlinear Science*, vol. 18, pp. 043106–15, Dec. 2008.

[67] M. A. Kon and L. Plaskota, "Information complexity of neural networks," *Neural Netw.*, vol. 13, no. 3, pp. 365–375, 2000.

[68] G. Tononi, "An information integration theory of consciousness," *BMC Neuroscience*, vol. 5, no. 1, p. 42, 2004.

[69] D. Balduzzi and G. Tononi, "Integrated information in discrete dynamical systems: Motivation and theoretical framework," *PLoS Computational Biology*, vol. 4, June 2008.

[70] R. A. Ince, R. Senatore, E. Arabzadeh, F. Montani, M. E. Diamond, and S. Panzeri, "Information-theoretic methods for studying population codes," *Neural Networks*, vol. In Press, Corrected Proof, 2010.

[71] R. Q. Quiroga and S. Panzeri, "Extracting information from neuronal populations: information theory and decoding approaches," *Nat Rev Neurosci*, vol. 10, pp. 173–185, Mar. 2009.

[72] A. Borst and F. E. Theunissen, "Information theory and neural coding," *Nature Neuroscience*, vol. 2, pp. 947–957, Nov. 1999. PMID: 10526332.

[73] M. Rubinov and O. Sporns, "Complex network measures of brain connectivity: Uses and interpretations," *NeuroImage*, vol. 52, pp. 1059–1069, Sept. 2010.

[74] C. E. Shannon, "A mathematical theory of communication," *Bell System Technical Journal*, vol. 27, pp. 379423, 625–56, Oct. 1948.

[75] D. M. MacKay and W. S. McCulloch, "The limiting information capacity of a neuronal link.," *Bull. Math. Biophys.*, vol. 14, pp. 127–135, 1952.

[76] J. J. Collins, C. C. Chow, and T. T. Imhoff, "Stochastic resonance without tuning," *Nature*, vol. 376, no. 6537, pp. 236–238, 1995.

[77] G. Tononi and O. Sporns, "Measuring information integration," *BMC Neuroscience*, vol. 4, no. 1, p. 31, 2003.

[78] G. Tononi, O. Sporns, and G. M. Edelman, "A measure for brain complexity: relating functional segregation and integration in the nervous system.," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 91, no. 11, p. 50335037, 1994. PMC43925.

[79] G. Tononi, G. M. Edelman, and O. Sporns, "Complexity and coherency: integrating information in the brain," *Trends in Cognitive Sciences*, vol. 2, pp. 474–484, Dec. 1998.

[80] G. Tononi, O. Sporns, and G. M. Edelman, "A complexity measure for selective matching of signals by the brain.," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 93, no. 8, p. 34223427, 1996. PMC39624.

[81] A. J. Bell and T. J. Sejnowski, "An information-maximization approach to blind separation and blind deconvolution," *Neural Computation*, vol. 7, no. 6, pp. 1129–1159, 1995. PMID: 7584893.

[82] A. Campa, P. D. Giudice, N. Parga, and J. Nadal, "Maximization of mutual information in a linear noisy network: a detailed study," *Network: Computation in Neural Systems*, vol. 6, no. 3, p. 449, 1995.

[83] R. Linsker, "Improved local learning rule for information maximization and related applications," *Neural Networks*, vol. 18, no. 3, pp. 261–265, 2005.

[84] D. P. Palomar and S. Verd, "Representation of mutual information via input estimates," Dec. 2008.

[85] D. Guo, S. Shamai, and S. Verdu, "Mutual information and minimum Mean-Square error in gaussian channels," *IEEE Transactions on Information Theory*, vol. 51, no. 4, pp. 1261–1282, 2005.

[86] B. Chen, J. Hu, H. Li, and Z. Sun, "Adaptive filtering under maximum mutual information criterion," *Neurocomputing*, vol. 71, pp. 3680–3684, Oct. 2008.

[87] F. Gabbiani, "Coding of time-varying signals in spike trains of linear and half-wave rectifying neurons," *Network: Computation in Neural Systems*, vol. 7, pp. 61–85, Jan. 1996.

[88] D. P. Palomar and S. Verd, "Representation of mutual information via input estimates," *IEEE Transactions on Information Theory*, vol. 53, no. 3, pp. 453–470, 2007.

[89] N. Mesgarani, S. V. David, J. B. Fritz, and S. A. Shamma, "Influence of context and behavior on stimulus reconstruction from neural activity in primary auditory cortex," *J Neurophysiol*, vol. 102, pp. 3329–3339, Dec. 2009.

[90] B. M. Broome, "Population coding and reconstruction of complex stimuli in the locust olfactory system," 2006.

[91] G. B. Stanley, "Recursive stimulus reconstruction algorithms for real-time implementation in neural ensembles," *Neurocomputing*, vol. 38-40, pp. 1703–1708, June 2001.

[92] A. Lazar and E. Pnevmatikakis, "Reconstruction of sensory stimuli encoded with Integrate-and-Fire neurons with random thresholds," *EURASIP Journal on Advances in Signal Processing*, vol. Volume 2009, 2009.

[93] A. Lazar and E. Pnevmatikakis, "Consistent recovery of sensory stimuli encoded with MIMO neural circuits," *Computational Intelligence and Neuroscience*, vol. Volume 2010, 2010.

[94] A. Das, R. Folland, N. G. Stocks, and E. L. Hines, "Stimulus reconstruction from neural spike trains: are conventional filters suitable for both periodic and aperiodic stimuli?," *Signal Process.*, vol. 86, no. 7, pp. 1720–1727, 2006.